
PLANT PALEOECOLOGY IN DEEP TIME¹

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ABSTRACT

The paleoecology of plants as a modern discipline, distinct from traditional floristics or biostratigraphy, has undergone an enormous expansion in the past 20 years. In addition to baseline studies characterizing extinct plants and plant assemblages in terms of their growth habits, environmental preferences, and patterns of association, paleoecology has converged on neoecology and represents a means to extend our basic understanding of the world and to contribute to the theoretical framework of ecology, writ large. Reconstruction of whole plants, including studies of physiology and developmental biology, and analyses of biomechanics have become mainstays of autecological studies. Assemblage studies now are informed by sophisticated taphonomic models that have helped guide sampling strategies and helped with the interpretation of statistical data. Linkages of assemblage patterns in space and time with sedimentology, geochemical proxies for atmospheric composition and climate, paleosol analyses, and increasingly refined geochronological and sequence stratigraphic data have permitted paleoecologists to examine rates and extents of vegetational response to environmental change and to time intervals of quiescent climatic conditions. Studies of plant-animal interaction, explicit consideration of phylogenetic information in assessing assemblage time-space dynamics, and examination of ecological structure in terms of developing metabolic scaling theory are all having direct impact on paleoecological as well as neoecological studies. The growth of paleoecology shows no sign of diminishment—closer linkages with neoecology are needed.

Key words: Environmental biology, paleobotany, paleoecology, taphonomy.

The discipline of ecology encompasses the characterization of multispecies systems, the description of their spatial and temporal dynamics, and the search for organizing principles and general models. Of course, any explanatory models developed from studies of modern systems should apply consistently to long-extinct ecological realms as well, if they are to claim generality. Thus, in the largest theoretical sense, ecology not only should, but must, include and integrate data from modern systems with those from the past. The richness of empirical neoecological studies, which include more observable system-level dimensions than paleoecology (not the least of which is the possibility of experimental manipulations), nonetheless is limited temporally. Paleontology provides access to biological phenomena on a wide spectrum of time scales. But, in contrast to neoecology, it has limited spatial resolution at finely resolved time scales, is restricted to comparative data only, and includes many systems that are composed of organisms about which biological understanding may be limited. However, neobiology and paleontology overlap in many ways and together

can be the basis for a robust understanding of the ways in which organisms respond and interact over short and long spans of time. Such responses may be either to environmental or biological crises of differing magnitudes, or both.

This paper is intended to review the broad field of plant paleoecology in the pre-Pleistocene, including the fundamental building blocks of the discipline, as well as considerations of the application of the basic data to problems of broader theoretical interest and importance. We do not believe that any caveat or apology is necessary for the various limitations presented by the fossil record. The matters at hand are: what can be done with the record; to what degree can its undoubted biases be understood, considered, and accounted for; how can one evaluate those data in real time to understand the ecological dynamics, preserved therein; and how can models based on extant systems be tested against that record? It is the intent of this contribution to provide a way into the literature of this rapidly growing, increasingly diverse field, while trying to identify the major areas of research, mature and just developing.

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MAJOR AREAS OF RESEARCH

Paleoecology is a discipline that includes research approaches that range from morphology and floristics, which might be considered the traditional strengths of paleobotany, to some that were embryonic 25 years ago, such as growth modeling, evaluation of physiological proxies, and linkages between biotic and abiotic studies (geochemistry, sedimentology, paleopedology). The immediate questions of interest in each of these areas vary considerably. The following discussion addresses what seem to be the major foci of current research. Basic systematic investigations remain the core of paleobotanical research, and the continuance and importance of those endeavors are implicit throughout this paper. Alpha systematics provides the basic language with which we describe multispecies systems, and phylogenetic analyses are an increasingly important part of ecological studies.

AUTECOLOGY

The reconstruction of past organisms, as much as possible as whole plants, is probably the fundamental building block of paleobotanical research and, with a twist, of paleoecological studies. The key that takes this endeavor into ecology is the step from systematics as the end goal and the move into the ever-growing focus on functional morphology, growth architecture, and whole-plant reproductive biology, which ultimately aims at understanding autecology in as much detail as possible. The real challenge in this research is to see the past on its own terms. In other words, the challenge is to imagine and allow for the possibility that extinct organisms may have functioned in ways not known today, and that such function will, or can, be revealed in the gross morphology of the organism.

FLORISTICS AND VEGETATION STUDIES

Description of fossil floras, along with basic morphology, is perhaps the longest-standing research area of paleobotany. Development of protocols to describe floras quantitatively, to sample them in ways that permit reconstruction of original vegetation, and to analyze them statistically, is a major area of study and a building block of larger studies of ecological dynamics in time and space.

RESOLUTION

Considerable effort has been devoted to taphonomy—the study of the fossil record and the processes that underlie its origin. Perhaps the most fundamental paleoecological question in taphonomy is that of spatio-temporal resolution. Before the record can be

used to address questions in ecology, *sensu lato*, it is necessary to consider the limitations of the record in candid detail.

DYNAMICS OF ECOSYSTEMS IN RESPONSE TO PERTURBATIONS

Paleontology may be able to contribute uniquely to ecology through the examination of multispecies assemblage dynamics over time intervals not accessible to neobiological analysis. The most publicly visible of these kinds of studies are those that examine biological responses to major environmental perturbations, such as catastrophic environmental change (brought on by such things as an asteroid impact or massive volcanism), major climate change (global to regional temperature increases or decreases linked to precipitation patterns), or linkages between biotic dynamics and changes in atmospheric composition. Presently, researchers are, or have been, focused on several time intervals of major extinction in Earth's history, and one can ask just how much can be generalized from any one of these. In other words, are there dependencies or contingencies unique to any system at any point in deep time that limit generalization from it alone? Is any one extinction interval unique, and thus, not of broader interest? Are there temporal trends suggesting the evolution of system-level responses through time?

ECOSYSTEM ASSEMBLY OVER SHORT AND LONG TIME SPANS

There has been a long-standing discussion in ecology about the existence of levels of organization above species populations, but can such systems even be circumscribed realistically? Is there the possibility of emergent properties in multispecies assemblages? Consider the early debate between adherents of the superorganism versus individualistic schools of Clements (1916) and Gleason (1926). A vast literature exists about the concept of equilibrium in ecological organization (e.g., MacArthur & Wilson, 1967), extending to the relationship between ecological stability and complexity (May, 1973), and systems ecology (Odom, 1983). Recent debate has centered on Hubbell's (2001) neutral theory of ecological organization, including such concepts as metacommunities (Holyoak et al., 2005) and assembly rules (Belyea & Lancaster, 1999; Weiher & Keddy, 1999). There also is increasing interest in the relationship between the historical-phylogenetic structure and the ecological architecture of assemblages of organisms (Shugart, 1997; Webb et al., 2002).

Paleontological data can be construed to indicate long periods of ecological persistence, even in the face of environmental fluctuations (e.g., Brett et al., 1996,

2007; DiMichele et al., 2004). And although not particularly couched in the terminology of assembly rules, it does appear that ecological systems underwent long periods of evolutionarily driven assembly, controlled by processes not unlike those proposed for very general rules of ecological assembly in space (compare Valentine [1980] with Belyea & Lancaster [1999]). If there are very general rules, to what extent are they taxon or assemblage specific?

More recently, intriguing work with great potential impact has been conducted on scaling relationships among plant-body sizes, metabolic rates, and ecological factors such as self-thinning of both populations and multispecific stands (e.g., Niklas & Enquist, 2001; Niklas et al., 2003), which may relate directly to the manner in which plants sort out resources within multispecies assemblages. Aspects of the first two topics have been investigated in various deep-time taxa (e.g., rhyniophytes and zosterophylls, cf. Roth-Nebelsick et al., 2000; Roth-Nebelsick, 2001; angiosperms, cf. Roth-Nebelsick et al., 2001) as well as in universal generalities (e.g., Roth-Nebelsick et al., 1994a, b), with the possibility of applying these results to assemblage-level communities over the Phanerozoic.

ARE THERE UNIQUE PATTERNS RECOGNIZABLE ONLY ON LONG TIME SCALES?

Are there kinds/types/classes of relationships between ecological and evolutionary dynamics that can be understood, or even simply recognized, only within the context of the geological-time rate spectrum (see below)? The recognition of such patterns will likely be an empirical outcome only of trends identified within the fossil record.

THE GEOLOGICAL-TIME RATE SPECTRUM

There is no single entity that can be characterized as Geological Time. Rather, the geological record preserves a wide spectrum of resolvable time intervals. Thus, the problem is one of time resolution. A major element of time resolution in the geological record is time averaging (see Behrensmeyer et al., 2000), which is more pronounced in the invertebrate and vertebrate fossil records than in that of plants.

The stratigraphic record includes plant-bearing beds of various attributes, each of which represents accumulation of debris within one original environment. Each genetic assemblage (the stratigraphic interval over which the assemblage is preserved) also can be considered to be a time layer of different irreducible temporal thicknesses. These may range from those preserved instantaneously (10^0 -year deposits), such as forest floors buried under volcanic

ashfalls (e.g., Wing et al., 1993), to those that are catchments of material accumulated over hundreds of years, such as tidal estuarine settings and packrat midden deposits (e.g., Mazon Creek, Pfefferkorn, 1979; Pearson & Betancourt, 2002), to many thousands of years, such as deposits of resistant material floated into marine depositional environments (London Clay, Reid & Chandler, 1933). The thickness of a rock unit is not related necessarily to the amount of time it encapsulates. Thus, the biological assemblage from a given deposit (bed or horizon) may have accumulated over some period of time that cannot be further subdivided, depending on the nature of the rock unit in which it is embedded. It may be temporally irreducible at the time scale over which the deposit accumulated, which is its level of depositional (or taphonomic) time averaging. Such deposits can be combined into meta-assemblages, each of which can encompass a hierarchy of time units of variable length. Such units can be described as artificially or analytically time averaged (Behrensmeyer & Hook, 1992). Consequently, any depositionally or analytically time-averaged fossil deposit can be analogized to a photographic snapshot of the fossil record but taken with variable shutter speed. These shutter speeds range from ultrafast, such as in situ burial of a forest-floor litter (e.g., Gastaldo et al., 2004b), to ultraslow, such as the diversity of Linnean families sampled globally and lumped into geological stage-level bins (Rees et al., 2002). In the latter case, we can imagine shadowy species moving in and out of the exposure, much like the ghosts of people in 19th-century long-exposure negatives. Thus, the geological record preserves, in natural and artificial packages, a broad spectrum of time resolution. These time packages can be combined in various ways and manipulated analytically and statistically, providing a very powerful tool rather than irresolvable obstruction.

APPROACHES TO THE STUDY OF PALEOECOLOGY

At its most fundamental level, plant paleoecology is built on studies of individual plants and reconstructions of plant assemblages. In each case, there are various, often high degrees of uncertainty that must be overcome or accommodated for credible interpretations to be made. Taphonomy plays a role at all levels of inference in structuring interpretations and must be considered explicitly as a key element in all paleoecological analyses.

PALEOAUTECOLOGY

Reconstruction of whole plants. Comparative morphology has long been the core of paleobotanical

research. The ultimate goal of this research is to elaborate and understand the history of plant life on Earth. However, because of their modular construction and open, continuous manner of growth, whole plants are rarely preserved, instead tending to fall apart into a variety of organs. Putting these plants back together is a challenge. Not only is the objective to determine what isolated fossil organs go together but, where possible, to determine such things as the timing of reproduction relative to the plant's growth and life history or to variations in its physical environment and, more removed, the proportions of biomass allocated to reproduction versus vegetative growth, to the extent this can be estimated.

Perhaps the greatest biofantasy of whole-plant reconstruction is the misconception that organ attachment is the only way to ascertain organ association in an acceptable scientific manner. It is necessary to recognize that reconstructions of fossil plants are hypotheses, subject to test and revision. The more explicitly they are reconstructed and the more clearly the bases for reconstruction are made known, the more rigorously they can be evaluated by the addition of new information. First of all, attachment hardly provides certainty of unique association (e.g., the stigmarian root systems of Paleozoic arborescent lycopsids, which are found in attachment or association with many different species of several genera of stems belonging in different families; Bateman et al., 1992). More important is the degree to which this perspective denies the basic probabilistic nature of the reconstruction process and the fundamentally inductive, statistical nature of science. Likelihood is the main means by which the reconstruction of extinct plants must proceed if we are ever to have more than a handful of species confidently reassembled. The underlying means for such reconstructions include recurrent association at sample sites, association at sites with only one kind of each organ, anatomical and morphological similarities among dispersed organs, and similarities in the morphology and anatomy of organ cuticles and epidermal cell patterns.

The most important point may be that in paleoecological analyses, it is necessary to work with a variably complete understanding of the biology of the organisms, and keep hypotheses congruent with what is known or what can be reasonably inferred from the data. Some recent examples of the application of these various approaches to whole-plant reconstruction are highlighted below. There are a relatively large number of plants, too many to cover exhaustively here, that have been completely or partially reconstructed by various means, but these still represent just a tiny

fraction of the plant species thought to have existed in the geological past.

Reconstruction from organ attachment is the most difficult of all kinds to undertake and requires attention to fine detail as well as a little luck. Perhaps the greatest abundance of whole plants is found among the early land plants of the Late Silurian and Early to Middle Devonian. Because of their simple morphologies, complete or nearly complete plants, including reproductive organs, often have been found and reconstructed. Such reconstructions have been effected directly and most often from compression fossils, some of which also have anatomical details preserved via permineralization. A few examples include the enigmatic fungus *Prototaxites* Dawson (Hueber, 2001; Boyce et al., 2007), the lycopsid *Sawdonia ornata* (Dawson) F. M. Hueber (Hueber, 1971), the trimerophyte *Pertica quadrifaria* Kasper & Andrews (Kasper & Andrews, 1972; Gensel & Andrews, 1984), and numerous plants from the classic Rhynie Chert in Scotland, which usually have been reconstructed by finding parts attached in series rather than as single whole plants (Paleobotanical Research Group, University of Münster, 2007). One of the most puzzling nearly whole plants is *Cooksonia* W. H. Lang, often touted as the earliest vascular land plant but known only from aerial parts (Edwards et al., 1992). Where were the prostrate axes to which these organs presumably were attached? Rothwell (1995) suggested that *Cooksonia* may have been a sporophyte incapable of a free-living existence, instead growing attached to a photosynthetic gametophyte, much like modern moss sporophytes and, thus, far from completely known morphologically. Gerrienne et al. (2006) found a cluster of Early Devonian *Cooksonia* axes attached to a thalloid-like pad and offered three possible interpretations, among which was the possibility that the axes represented sporophytes attached to a gametophyte. This hypothesis has been given biomechanical and physiological support by Boyce (2006), who demonstrated that most *Cooksonia* species are too narrow to have had sufficient photosynthetic tissues to sustain themselves independently.

The earliest fully reconstructed seed plant, *Elkinsia* Rothwell, Scheckler & Gillespie (Rothwell & Serbet, 1992; Serbet & Rothwell, 1992), is known to a degree that the timing and extent of reproductive allocation can be evaluated (e.g., Rothwell & Scheckler, 1985; Scheckler, 1986). Reconstructions are not limited to members of the understory; creeping ground cover and/or lianas are also well represented (Manchester & Zavada, 1987; Krings & Kerp, 1999). The late Paleozoic gymnosperm *Callistophyton* Delevoryas (Rothwell, 1981) may be one of the most fully reconstructed plants of the entire geological record.

The detailed nature of Rothwell's (1981) reconstruction, based on permineralized anatomically preserved specimens, has permitted some revision based on findings from compression fossils (Galtier & Béthoux, 2002), illustrating the concept of reconstruction as testable hypothesis.

Whole-plant preservation is most likely for small plants. For example, the only known herbaceous conifer, *Aethophyllum* Brongn. from the Triassic, was reconstructed from a complete plant, a finding made perhaps more likely because of the small stature of the plant (Rothwell et al., 2000). Some other whole plants found in the fossil record include the isoetalean lycopsids *Clevelandodendron* Chitaley & Pigg (1996), of Late Devonian age, and *Chaloneria* Pigg & Rothwell (1983) and *Hartsellea* Gastaldo, Gibson & Blanton-Hooks (2006) of Pennsylvanian age, all with pole-like growth forms and comose base. The former is a single specimen terminating in a fertile zone, whereas *Chaloneria* was put together from a number of variably complete specimens, terminating either in a fertile zone or with intercalated fertile and sterile zones. *Hartsellea*, on the other hand, was preserved erect and in situ within a back-barrier marsh. Escapa and Cúneo (2005) reconstructed the early equisetophyte *Peltotheca furcata* Escapa & Cúneo from segments of plants that permitted linkage of reproductive and vegetative parts. Small aquatic plants occur in taphonomic settings that favor intact preservation. Examples include *Archaeofructus liaoningensis* Sun, Dilcher, Zheng & Zhou, an aquatic angiosperm (Sun et al., 2002a), and *Hydropteris pinnata* Rothwell & Stockey (1994), a heterosperous aquatic fern, each proposed as the basis of new families of phylogenetic significance.

Larger shrubs and/or trees are extremely difficult to find preserved as whole plants. Rare discoveries of juveniles (e.g., Stidd & Phillips, 1968) can provide information about development and assist in the reconstruction of adult plants known only from isolated organs. The discovery of whole trees does occur occasionally, however. For example, Wnuk and Pfefferkorn (1984) discovered a forest of lycopsid trees with medullosan understory blown down during a storm and buried in place. The medullosans conformed to two growth habits. In one, trees were solitary, upright in growth stature, with trunks more than 20 cm in diameter and less than 5 m in height. Fronds were closely spaced, about 10 per meter of stem length, and were curved downward after death, suggesting development of a skirt, a morphological means of protection against epiphytes and vines. The other form was found in groups, suggestive of thickets in which the large fronds intertwined, allowing the trees to be mutually supporting. Stems were flexuose,

up to 13 cm in diameter and greater than 5 m in height, with widely spaced fronds that appear to have been shed regularly rather than remaining attached. Pfefferkorn et al. (1984) evaluated published reconstructions of medullosans, which show a wide range of variation on the flexuose versus upright habit and determined that most were considerably inaccurate. Unfortunately, while revealing a great deal about medullosan growth habits, the actual foliage of these plants was not preserved attached; hence, taxonomic identity could not be established.

Partial reconstructions from attachment may sometimes have greater ecological significance than full reconstructions. Consider, for example, the Mesozoic cycadeoids, reconstructed primarily from silicified trunks, in which mature strobili were found at developmental states suggesting monocarpic (or "pseudomonocarpic") reproduction (Wieland, 1921). Similarly, the reconstruction of the false-trunk fern *Tempskya* Corda from the Cretaceous reveals a growth form unknown among ferns or seed plants today (Andrews & Kern, 1947). Fortuitous connection of stem/wood, sepals, and stamens with included pollen permitted the reconstruction of several plants by Manchester and colleagues (Manchester & Crane, 1983; Manchester et al., 1986; Manchester, 1989); we consider these to be "partial" reconstructions because the attached parts are from branches of presumed trees, and because the suite of organs found in attachment, although representing vegetative and reproductive parts, is an incomplete set.

Probabalistic means of assembling whole plants from dispersed organs, rather than through organ attachment, have produced a large number of reconstructions and given us considerable insight into the biologies of the plants. Paleozoic plants, in particular, are challenging because they generally have no close living relatives. Pennsylvanian arborescent lycopsid reconstructions, for example, historically illustrate egregious errors, particularly as related to the dynamic biology of the plants. Individually or in forest stands, these trees are almost always reconstructed along the lines of angiosperms. Trees are given light-capturing crowns and frequently are shown tipped over with their root bases in the air, presumably from blowdowns. However, evaluation of the development of these plants reveals dramatic architectural changes from juvenile to reproductively mature adult, which has major implications for individual plant and landscape reconstructions. Stands of these plants probably looked little like their representation in dioramas and paintings. Fossil data suggest two major growth forms, with different reproductive biologies. In one type, which is the most widely reconstructed, individual trees spent nearly all

of their lives as unbranched poles, forming a crown only at the end of tree life, which was determinate (Andrews & Murdy, 1958; Eggert, 1960). Anatomical (DiMichele, 1979) and compression (Wnuk & Pfefferkorn, 1987) studies indicate that cones were produced on these plants among the branches in the crown during the terminal phases of growth, rendering them effectively monocarpic (Bateman & DiMichele, 1991; Bateman, 1994). That cones were borne only in the terminal-phase crown suggests that height and tree crowns had little to do with light capture and much to do with dispersal of reproductive organs (DiMichele & Phillips, 1985; Phillips & DiMichele, 1992). The other growth architecture consisted of a determinate monopodial trunk bearing determinate deciduous lateral branches (DiMichele, 1980). Cones were borne among the lateral branches in some taxa or were borne directly on the trunk in others. In either case, the trees were polycarpic. The small, deciduous lateral branch systems were too small to account for much light capture in most species with this life strategy.

These peculiar trees had tenacious root systems that spread far from the trunk at shallow depths. The longest recorded stigmarian axis approaches 13 m. Neither of the authors have ever seen a tipped-up tree in their many visits to mines where stumps of these trees are exposed (e.g., Gastaldo, 1986; DiMichele & DeMaris, 1987; Wnuk & Pfefferkorn, 1987; DiMichele et al., 1996; Gastaldo et al., 2004a) nor have they read of any such tip-ups reported in the literature. Yet, uprooted lycopsids are staple elements of Carboniferous swamp reconstructions, implying that blowdowns and uprooting, for which there is no evidence, were parts of the disturbance mode in such systems.

Finally, anatomical studies of arborescent lycopsids raise certain matters with regard to their physiology (Phillips & DiMichele, 1992). The lack of a clear phloem connection between root and shoot, the generally limited phloem throughout the plant's aerial shoot, the leaf-like rootlets borne on the stigmarian axes, and the long leaves on stems and cones, are all consistent with extremely localized use of photosynthate and perhaps even self-supporting root systems in terms of carbon fixation. The purpose of this long discussion is to illustrate how much can be known and understood about fossil species from disconnected organs when intense work by many investigators is integrated into a series of reconstructions of considerable, though hardly absolute, certainty. This is even more remarkable given that a whole lepidodendrid lycopsid tree has never been found intact from top to bottom.

Disconnected organs can be linked into nearly living whole plants by using common features of gross

morphology. An example of this comes from the work of Krings and colleagues. In a series of papers (summarized in Krings et al., 2003), they used cuticular features and gross morphology to link disconnected organs and reconstruct liana and vine-like habits in several species of Pennsylvanian-age pteridosperms. They detail a variety of climbing mechanisms, from hooks to pads to tendrils, that have structural analogues in taxa of other clades. In addition, they note much higher relative abundances and diversities of these plants in Late Pennsylvanian environments compared to environmentally similar Early and Middle Pennsylvanian tropical ecosystems. Clearly, there were major changes in the dynamics of these tropical forests, associated with major species turnover and change from lycopsid to tree fern canopy dominance, that favored the increase in vine abundance (possibly disturbance and patchiness of the forests; see Gastaldo et al., 2004b).

Strong patterns of organ association also allow whole plants to be reconstructed from disconnected organs, especially when an assemblage consists only of one of each organ type attributable to a particular higher-level group of plants. This is strengthened further by repeated occurrences of organ associations at multiple collecting sites. An example of this comes from the work of Kvaček et al. (2005), who proposed a reconstruction of a Late Cretaceous ginkgoalean consisting of the following dispersed organs: wood (*Ginkgoxylon greutii* Pons & Vozenin-Serra), short shoots (*Pecinovi cladus kvacekii* Falcon-Lang), leaves (*Eretmophyllum obtusum* (Velen.) Kvaček), ovuliferous organs (*Nehvizdyella bipartita* Kvaček, Falcon-Lang & Dašková), and pollen (*Cycadopites* Wodehouse). They found this same association at four different collecting sites in consort with organs of other types, none of which were ginkgoalean in affinity. In addition, due to anatomical preservation of some remains, they were able to link the various organs sequentially in terms of their relative spatio-structural position on the plant. Finally, these plant remains occurred in a specific, recurrent lithofacies, indicative of peat deposits formed in salt marshes (making this the first described salt-tolerant mangrove ginkgophyte and indicating that the biology of this plant cannot be understood by analogy primarily with modern representatives, of which there is only one in the case of ginkgophytes). Other examples include *Archaeanthus linnenbergeri* Dilcher & Crane, an early angiosperm, reconstructed from partial attachment and associated organs, using anatomical similarities and the presence of distinctive resin bodies (Dilcher & Crane, 1984), and *Pentoxylon* Sahni, reconstructed from repeated associations of leaves, stems, and reproductive organs found in detailed sedimentolog-

ical context (Howe & Cantrill, 2001). Examples of organ linkage into whole or partial plants can be found in many groups and, remembering the hypothetical nature of reconstructions, is probably one of the strongest and most likely means of developing such associations.

The use of large samples from single sites also facilitates the reassembly of whole plants from isolated and partially preserved organs. An example of this is the work of Hernandez-Castillo on the early walchian conifer *Thucydia mahoningensis* Hernandez-Castillo, Rothwell & Mapes (Hernandez-Castillo et al., 2001, 2003). Hernandez-Castillo and colleagues were able to reconstruct this species, including its growth habit, from a large population of fragmentary compression fossils, some with preserved anatomy, including leafy branches, stems, and reproductive organs, and one specimen with branches attached to a stem segment. They concluded that early walchian conifers were considerably smaller than generally envisioned, perhaps reaching only 2 m in height, with architecture much like juveniles of the araucarian conifer *Araucaria heterophylla* (Salisb.) Franco (Norfolk Island Pine). Similar reconstructions of walchians, although of larger size, have been suggested by Ziegler et al. (2002a) based on much smaller populations of fossils. The larger-scale study informs and adds confidence to these other investigations and interpretations.

Whole-plant concepts can also be created by direct comparison with living descendants or close relatives. This is especially true of deciduous angiosperms, where isolated leaves make up nearly all of their fossil record, and post-Paleozoic conifers, where many groups have living descendants. It is also true of ferns, where most of the modern families appeared in the Mesozoic (Rothwell, 1994; Collinson, 2002; van Konijnenburg-van Cittert, 2002a, b). Through a combination of morphologic and taphonomic/sedimentologic analyses and comparison with modern species, a complex of early Tertiary elms has been characterized and examined with regard to changing ecological preferences through time (Burnham, 1983, 1986). Taxa were found to have high degrees of ecological fidelity over millions of years. For conifers, consider the Eocene age mummified *Metasequoia* Hu & W. C. Cheng forests found north of the Arctic Circle in Canada (Williams et al., 2003a, b). Here, in situ stumps were found in association with mummified logs and thick beds of peat containing three-dimensionally preserved, but disconnected, cones and leaves in profusion, permitting reconstruction of plant biology and landscape structure. These plants can be compared directly to living *Metasequoia* from which a wide range of inferences is possible, including

physiology (LePage et al., 2005). An example from Mesozoic ferns is that of Skog and Dilcher (1994) from the Cretaceous Dakota Formation. These deposits include species of the fern families Schizaeaceae, Matoniaceae, and Gleicheniaceae in wetland deposits, where they remained dominant even as angiosperms were increasing in other habitats. Today, members of these families form expansive tropical fern brakes in open areas or occur as undergrowth in more open forests. Direct evidence for this in the past is limited, but Skog and Dilcher (1994) infer this as a likely habit for the fossil taxa by analogy to these modern situations. They also propose that some Dicksoniaceae may have formed dense thickets, based solely on analogy to modern forms. In the absence of grasses, it has been suggested that ferns played a similar role, forming extensive areas of ground cover (LePage & Pfefferkorn, 2000).

Reproductive biology. The study of reproductive biology is a central part of both modern and fossil plant ecology. The most common approach, based on sheer numbers of published papers, has been the study of reproductive organs as isolated entities, generally placed within a particular evolutionary lineage or higher taxon but not tied to a particular whole-plant species (e.g., Taylor, 1982). Such studies have been compiled into analyses of patterns through time, most often with a focus on morphological evolutionary history (e.g., Taylor, 1965). Other studies have focused on functional morphology of reproductive organs, with a particular focus on seeds and pollination biology (e.g., Rothwell, 1972). Some of these studies have been experimental, using physical models, sometimes including mathematical modeling as a component (e.g., Niklas, 1981). A few analyses have looked at the distribution and relative abundances of reproductive versus vegetative organs of single species in attempts to estimate reproductive allocation and dispersal behaviors (e.g., Schwendemann et al., 2007).

The study of reproductive organs occupies too much of the literature to be detailed here. However, some compilations include Taylor (1978) on Paleozoic seed-fern pollen, Millay and Taylor (1979) and Rothwell and Eggert (1986) on Paleozoic seed-fern pollen organs, Tiffney (1986) and Sims (2000) on the distribution of seed sizes and dispersal syndromes through geologic time, Tiffney (1994, 1999) or Gee (2005) on seeds and fruits from Tertiary deposits, Crookall's (1976) summary of Late Carboniferous seeds, the massive compilation of seeds and fruits in the Eocene London Clay flora (Reid & Chandler, 1933; Collinson, 1984), and the compilation of late Paleozoic marattialean reproductive organs by Millay

(1979). In some instances, isolated reproductive organs can yield insights into likely pollination mechanisms, especially when comparisons can be made to extant relatives (Klavins et al., 2003).

Pennsylvanian arborescent lycopoid reproduction is understood in some detail. This is made possible by a wide range of studies of the structure and function of microsporangiate and megasporangiate cones (e.g., Brack-Hanes, 1978; Phillips, 1979; Brack-Hanes & Thomas, 1983; Pigg, 1983), linkages between microsporangiate cones and dispersed spores (which also permits differentiation of species from peat vs. clastic substrates [Willard, 1989a, b]), linkages between parent plants and reproductive organs (see Bateman et al., 1992, for summary), and morphological studies, as detailed above, that tied together growth architecture and reproductive patterns (DiMichele & Phillips, 1985; Phillips & DiMichele, 1992). Quantitative studies of coal balls (permineralized peat) from Pennsylvanian-age coals (e.g., Phillips et al., 1977; Phillips & DiMichele, 1981) have permitted coarse-grained studies of propagule distribution patterns; comparison of the distribution of certain seed-like megasporangiate units with vegetative parts of the parent plants (*Lepidocarpon* Williamson vs. *Lepidophloios* Sternberg) demonstrates that the propagules are dispersed more widely than vegetative material, consistent with distribution by flotation under aquatic swamp conditions and an invasive distribution strategy. Once more, this kind of analysis is made possible by a combination of detailed morphological analyses, whole-plant reconstructions based on likelihood of association, and study of statistical patterns of plant distribution in time and space.

The ecology of reproduction in ferns is facilitated by the common presence of spore-producing organs in intimate association with laminate, photosynthetic foliage. In addition, it is often possible to make direct comparisons between ancient and modern fern biology (Page, 2002) because many extant fern lineages were in existence during the Mesozoic, and, additionally, all ferns share certain reproductive and life-history traits. The late Paleozoic marattialean ferns, for example, were dominant elements of wetland ecosystems (Phillips et al., 1985) and are very well known morphologically, from both anatomical (coal-ball) studies and compression-impression fossil analyses. More cheaply constructed in terms of carbon allocation than any other group of Pennsylvanian wetland plants (Baker & DiMichele, 1997), with tree habit made possible by a mantle of adventitious roots filled with airspaces (Ehret & Phillips, 1977), these plants produced massive numbers of highly dispersed spores, permitting them

to act as invasive weeds as well as forest canopy dominants (DiMichele & Phillips, 2002). Many of the basal extant families of filicalean ferns arose during the early Mesozoic (Tidwell & Ash, 1994; van Konijnenburg-van Cittert, 2002a, b), their importance tapering off into the later Mesozoic and Cenozoic (Collinson, 2001; Wang, 2002). However, during the later Mesozoic, ferns remained ecologically dominant in many habitats and in many ecological roles, from colonizers of disturbed substrates to biomass dominants (e.g., Wing et al., 1993; van Konijnenburg-van Cittert, 2002a, b). Cenozoic ferns are subordinate to angiosperms in most floras from this time interval, leading to a comparatively understudied record relative to ferns from older eras (see summary of Collinson, 2002), but are known to have occupied a range of habitats similar to extant ferns.

In some instances, it takes years to put together a picture of the biology of a fossil plant or group of plants. Reproductive biology is generally the most elusive part of such a reconstruction. A case in point is the biology of the Bennettitales, an important and diverse group of plants in many Mesozoic ecosystems that included both outcrossing and potentially inbreeding species. Members of the Cycadeoidaceae were considered to be monocarpic (Wieland, 1921) and likely animal, possibly beetle, pollinated (Crepet, 1974). In some species of the Williamsoniaceae, however, anatomical evidence supports wind pollination, seed dormancy, and outcrossing (Stockey & Rothwell, 2003).

Modeling studies of reproductive dynamics have been applied mainly to early land plants, where modern analogues of the fossil morphologies are lacking. Niklas (1981, 1983a) built scaled-up models of Late Devonian and Mississippian seeds and bombarded them with jumbo-sized, model pollen grains in wind tunnels. The seeds studied varied from those with completely unfused integuments and megasporangial modifications that facilitate pollen capture, described as hydrasperman reproduction (Rothwell, 1986), to those with closed integuments, some further enclosed in cupules. Such models allow direct testing of functional morphological scenarios. They also make specific predictions about how pollination biology of such ovules may have functioned, which can be tested against the fossil record (see comment and response from Rothwell & Taylor, 1982; Niklas, 1983b). Preliminary studies also have been carried out on pollen sedimentation rates, which have permitted testing of hypotheses about wind versus animal pollination in certain groups. For example, how do large medullosan pteridosperm pollen grains settle in liquids, such as pollen drops, relative to saccate pollen types, such as those

produced by early conifers (Schwendemann et al., 2007)?

Biomechanical attributes of fossil plants. Study of the biomechanical properties of plant tissues has permitted insights into growth and development that are difficult to attain by other means of reconstruction. Such approaches can be of great value even when only parts of plants can be evaluated (e.g., Speck, 1994). The grouping and distribution within the stem of anatomically preserved tissues can be analyzed and compared directly with modern analogues because of the physical nature of the system (Niklas, 1992).

Study of the growth architecture of the Pennsylvanian-age plant, *Sphenophyllum oblongifolium* (Germar & Kaulfuss) Unger by Galtier and Daviero (1999) illustrates a statistical approach to understanding plant growth form and its structural and ecological implications. By examining patterns of internode length, axis diameter, and leaf length, these authors were able to examine the growth ontogeny of the plant and infer scrambling, thicket-forming habit.

An example of contrasting approaches with convergent conclusions is demonstrated for the relatively well-known Middle Devonian aneurophytalean progymnosperm *Tetraxylopteris schmidtii* Beck (Beck, 1957), which was originally reconstructed as a small tree, perhaps as much as 3 m in height. Speck and Rowe (2003) studied the plant's anatomy in addition to growth architecture and concluded that it was not likely to have been self-supporting. In a more traditional but extremely detailed morphological analysis of a related species, *T. reposana* Hammond & Berry, the authors (2005) came to a similar conclusion regarding growth habit. *Tetraxylopteris* Beck is now considered to have been a small bushy plant that formed dense thickets of interlocking branches. Fertile branches were likely borne on the more distal parts of the plant, where the sporangia would be most exposed. The combination of such studies provides insight into this entire group of extinct plants and suggests that this kind of growth form may have been characteristic of the clade (Speck & Rowe, 2003).

Similar approaches have been used to examine growth form of the Calamopityaceae, an extinct group of Mississippian pteridosperms. These were small plants with limited secondary xylem, probably scrambling ground cover and/or vines. Rowe et al. (1993) analyzed their stem architecture and determined that internodal distances are relatively short in large-diameter stems but become increasingly long in smaller-diameter stems. The decrease is so dramatic that the small stems appear to have been incapable of self-support. Hence, it is possible that the mature

plant had an upright or corm-like basal portion with a trailing or semi-self-supporting upper part. In contrast, Speck and Rowe (1994) conducted a biomechanical analysis of the much larger Mississippian pteridosperm *Pitus dayi* Gordon and concluded that it was certainly self-supporting and abscised its frond-like leaves.

The potential power of biomechanical studies is additive. In isolation, they may enhance understanding of the ecologies of individual plants. But, in aggregate, they allow those individual ecological insights to take on considerably greater significance. Most multi-taxon biomechanical and architectural studies, especially those that look broadly across clades, have been aimed at understanding evolutionary phenomena (e.g., Niklas, 1999). However, such studies can also be of fundamental importance in ecology. Consider the study of Niklas and Speck (2001), who investigated the evolution of structural safety factors to wind shear in early land plants, revealing distinct trends both through time and with regard to plant height, largely independent of clade membership. The phylogenetic independence of the trends is consistent with biomechanical properties of common structural elements and their stereotypical spatial deployment within plant stems. This approach opens the door to the estimation of wind effects in the context of its effect on stand density, plant morphology, and the relationships between wind, plant architecture, and reproductive strategies.

PALEOSYNECOLOGY—PUTTING TOGETHER A COMMUNITY

The reconstruction of past assemblages of plants is another of the central, and traditional, pursuits of terrestrial plant paleoecology. Until recently, such endeavors could be described broadly as floristics, the elaboration of a taxonomic list from one or more collecting sites in the same bed/sedimentological unit, or even from a time interval of variably long duration, with the underlying assumption being that they were growing in common, part of the same life assemblage. Often, visual or descriptive renderings of the inferred parent vegetation were made, generally representative of the species pool or even of the regional biome, although not explicitly stated or even recognized as such (e.g., Davies, 1929; Becker, 1972). The addition of sedimentological context to species lists greatly refines such studies, restricting the inferred assemblages to those taxa that grew in or proximate to the environment of deposition, thus making the list more representative of actual life communities (e.g., Hickey & Doyle, 1977; Scott, 1978; Wing, 1984; Spicer et al., 2002). The most representative reconstructions, both visual and statistical, are based on data, quantitative

and presence-absence, from field samples. The correlation of sedimentary settings with quantitative floristic composition, at as finely resolved a taxonomic level as possible, provides the closest approximation of the original vegetation. We will focus on such approaches. It should be evident from the following discussion that a thorough understanding of the sedimentologic, stratigraphic, and taphonomic framework is essential prior to any attempt to make paleoecological inferences from plant-fossil assemblages in space or time.

Taphonomic considerations. Vegetation and landscapes vary enormously in systematic composition, plant density, and vegetational architecture on continental spatial scales, influenced by climatic, topographic, and edaphic controls. Yet, plant remains are preserved only under a relatively strict sedimentological and geochemical subset of all possible conditions (Gastaldo, 1992a, 1994; Spicer, 1988, 1989). These conditions greatly reduce the likelihood of fossilization for many types of plant assemblages, depending on landscape position and climate. Additionally, there are a limited number of sites within any landscape where the potential exists to preserve plant parts because this can occur only in depositional regimes where: (1) dysoxia and/or anoxia prevails (i.e., at the sediment-water interface in a lake system); (2) micro-environmental geochemical gradients are strong (e.g., fluvial channel-bar troughs, Gastaldo et al., 1995); (3) resistant and diagnostic phytoclasts persist unaltered long after decay has removed all soft tissues (e.g., phytoliths, Strömberg, 2002; palynomorphs, Traverse, 1994); or (4) buried assemblages are maintained below the regional water table preventing oxidation and decay over the long term (10^3 – 10^8 -year time scale; Gastaldo & Demko, 2005). In the majority of instances, biomass is fated to be recycled within the carbon cycle by the living biota—this is the rule rather than the exception.

The disarticulation of vegetative and reproductive structures, along with their tendency to degrade quickly, on the order of weeks (e.g., flowers and leaves), months (leaves), or years to several decades (wood, fruits, and seeds; Burnham, 1993b), presents some advantages and disadvantages when attempting to reconstruct anything, from a single plant to the original plant community or a landscape mosaic. It is especially rare for dispersal structures (e.g., seeds or spores) to be found attached to higher vascular plants. But, when such structures are found attached, it provides direct evidence for the operation of traumatic, as opposed to physiological processes, in the origin of the assemblage (Gastaldo, 1992a, 1994). It is well documented from neoecological and experimental

taphonomic investigations that decay rates not only differ within taxa of a single clade or between various clades, but also under different climatic conditions (Gastaldo & Staub, 1999) and even within microhabitats under the same general climatic regime (Bray & Gorham, 1964). Additionally, the degree of similarity between a standing forest and the litter it produces may vary greatly and is not necessarily taxonomically proportional (including forest-floor litters; Burnham, 1989, 1997; Burnham et al., 1992), but depends on physiology and growth strategy (Gastaldo, 1992a). Yet, because decay rates of most plant parts are extremely rapid when compared with hard parts of invertebrates or vertebrates, it is possible to identify many of the constraining mechanisms and processes responsible for preservation of an assemblage. In addition, means have been developed to estimate the taxonomic diversity of the source vegetation (e.g., Burnham, 1993a; Gastaldo et al., 2004a). Hence, nearly all plant assemblages can provide what amounts to a T_0 estimate of the taxonomic composition of the source community and some degree of relative abundance of the source plants (this is more the case when leaves and other soft-tissue structures are preserved). It is true that certain resistant plant parts may be reworked, such as woody debris, charcoal, and palynomorphs, within particular depositional systems or particular intervals within stratigraphic sequences. Criteria have been developed, however, that allow for recognition of such recycled parts (e.g., wood-clast rounding, Gastaldo, 1994; change in palynomorph fluorescence, Traverse, 1988), the presence of which can thus be eliminated from consideration when evaluating an accumulation of plant parts from an identified transported assemblage.

There is an overrepresentation of wetland communities in the plant fossil record because these are in closest proximity to depositional regimes with the highest probability of preservation. Thus, such wetlands, particularly in the pre-Neogene, will account for the most fossils in autochthonous and parautochthonous assemblages. In situ, or autochthonous, assemblages are deposits of high importance and significance from which we can gain our greatest insights into community composition and spatial organization within the landscape mosaic. These assemblages consist of plant parts buried within the site where the source plants grew (Behrensmeyer & Hook, 1992). In general, there is little or no transportation of plant parts into or out of the area of burial, although there may be palynological contribution from outside the immediate area, especially if the source plants are wind pollinated. Hence, litters buried below the sediment-air interface, particularly below the mean water table, represent

those specimens capable of being preserved in the fossil record. Not all taxa contribute biomass equally to a litter assemblage. The contribution of any taxon may be a function of physiology, climate stress, or growth strategy, and the fidelity of the community within microhabitats of a landscape also may vary. For example, Burnham (1989: table IV, p. 16) found within a paratropical floodplain that the percentage of local species in the leaf litters, those within 100 m of the sample site, ranged from 45%–63%. The time at which litter is buried can further limit the fidelity of an assemblage, considering that different taxa contribute different proportions of their vegetative and/or reproductive structures during any growth year (Bray & Gorham, 1964), and that those proportions may vary seasonally and annually.

In particular depositional settings, such as within intermontane Tertiary sequences, care must be taken to differentiate the components actually preserved in situ from those that may have been transported downslope via various mechanisms, e.g., mudflows or lahars (Fritz, 1980a, b, 1981). Criteria have been developed to distinguish in situ from transported erect, root-laden trunks (Fritz, 1980b; Fritz & Harrison, 1985; Gastaldo, 1984, 1999). In coastal plains, such elements will be found in fluvial sediments and will have diagnostic features including root-encapsulated soil that may bear extrabasinal clasts (e.g., Liu & Gastaldo, 1992a; Gastaldo & Degges, 2007). Autochthonous burial can be instantaneous when entombment is the result of volcanoclastic ashfall (e.g., Burnham & Spicer, 1986; Wing et al., 1993), or over a period of days to months when increased sedimentation rate accompanies a change in local or regional base level (e.g., Ellis et al., 2003), which, in some instances, may be the result of coseismic subsidence (e.g., Gastaldo et al., 2004a).

Paraautochthonous assemblages (Behrensmeyer et al., 2000) consist of disarticulated parts that have been transported some distance from the parental vegetation but not outside of the landscape setting in which they grew. Such assemblages most often are found within floodplain lakes (Rich, 1989; Gastaldo et al., 1989, 1998; Howe & Cantrill, 2001), but also in fluvial channel bedload and bar deposits depending on the fluvial dynamics and aerial extent of the vegetational unit across the landscape. In general, plant parts preserved in fluvio-lacustrine settings are derived from vegetation directly adjacent to and fringing the body of water. But in such environments, the potential exists for the assemblage to include allochthonous elements that have been transported greater distances, depending on the geographical and altitudinal position of the lake (e.g., Spicer & Wolfe, 1987) and the proximity of tributaries debouching into

principal river channels (e.g., Gastaldo et al., 1987). Hence, it is imperative that an integrated geologic, taphonomic, and paleontologic approach be used to understand any assemblage prior to interpretation.

Allochthonous assemblages warrant caution when attempting to address certain paleoecological questions, although they may provide the only insight into the plants living in extrabasinal (Pfefferkorn, 1980) settings. In an intermontane lake deposit of Tertiary age (Taggart & Cross, 2000), it proved difficult to separate the plant parts originating in the fringing vegetation surrounding the lake from those transported into the lake from outside the area, particularly because all plant parts were transported as suspension-load debris. Use of phytoclasts as taphonomic features (e.g., bedload vs. suspension-load transported modification) in Gilbert-type delta-front deposits provided a means by which such local versus more regional contribution could be assessed (Spicer & Wolf, 1987). Using such data in conjunction with samples from other proximal and distal lake sites from the same geographic region, of the same approximate age, and formed under similar climatic conditions can permit assessment of the proportional contribution from different communities within the landscape to any given deposit. In assemblages preserved in offshore marine lowstand deposits (lowstand systems tract in the terminology of sequence stratigraphy), shore-fringing and more distal vegetation will be mixed and difficult to differentiate, thus limiting interpretation of the flora to regional spatial scales (e.g., Mapes, 1985; Rothwell et al., 1996). Often, the regional components of such floras are unknown in other parts of the stratigraphic sequence.

Sedimentary sequences, climate, and eustacy. The sedimentary context of a fossil plant assemblage is a crucial part of the equation that must be accounted for when using the record for paleoecological analyses. Often, these data are restricted to reports of the depositional environment (facies) and/or regional setting (correlative facies associations). But, without an analysis of the sedimentary sequence at a finer scale, it is possible to overlook pertinent information relevant to understanding the genesis of a plant-bearing deposit or rock sequence (Galloway & Hobday, 1996) or the interpretation of the fossil assemblage itself (Falcon-Lang & Bashforth, 2004; Gastaldo et al., 2005; Falcon-Lang, 2006).

Isotaphonomic assemblages (Behrensmeyer et al., 2000) must be distinguished and used when the paleoecological questions concern changes in taxonomic dominance or richness patterns in space or time. The identification of the sedimentary facies within a particular depositional regime, and the

taphonomic processes associated with that setting, provide the basis for comparison of communities. It is not sufficient to describe only the stratigraphic position or sediment matrix of the assemblage, because each of these criteria varies within a landscape. For example, Gastaldo et al. (1995) demonstrated that not all Carboniferous roof-shale floras preserved in coastal lowlands originate in the same way. Under specific depositional settings, these floras may be allochthonous, parautochthonous, or autochthonous, with the latter either preserving the ultimate peat-mire community (e.g., Gastaldo et al., 2004b; DiMichele et al., 2007) or a community that grew in a mineral substrate, unrelated to peat formation (e.g., Gastaldo, 1987; Falcon-Lang, 2006). The disparity in absolute time represented within such assemblages (e.g., coal-ball permineralized peats vs. buried-in-place clastic swamp vegetation) may be on the order of 10–100,000 years, depending on the combination of depositional and analytical time averaging. The same disparity holds true for floras preserved within the seatearth (paleosol) beneath a coal bed (Staub & Gastaldo, 2003).

The relative completeness of depositional sequences differs dramatically from continental to marine basins. Continental stratigraphies are the most incomplete, highly dependent on tectonic regime, basinal dynamics, and climate (Shanley & McCabe, 1994), with resolution varying within and between depositional environments (e.g., Pelletier & Turcotte, 1997; Lowenstein et al., 2003). Sediment transport from a source area is controlled by variations in long-term climate patterns, particularly the timing and amount of yearly rainfall (Cecil & DuLong, 2003). Similarly, rainfall patterns strongly control the distribution of plant communities. Thus, there must be a coincidence of plant preservation with periods of sediment transport, adequate physical accommodation space, and geochemical conditions that promote plant-part preservation rather than decay.

Although it may seem counterintuitive at first, little sediment is generated and transported in most environments wherever wet, humid to perhumid (rainfall 10–12 months/year; Cecil et al., 2003) climates prevail and precipitation exceeds evaporation and evapo-transpiration. Under these conditions, the landscape is covered by a multi-tiered vegetation. Extensive rooting at various levels within the soil profile binds sediments and prevents large-scale soil erosion and sediment transport down gradient to depositional environments. Pedogenesis (especially formation of podzols to laterites) is the principal process operating across the landscape under such climatic conditions (Parrish et al., 1993; Sellwood & Price, 1993). If soils contain sufficient proportions of

expandable (swelling) clays, stagnant paludal conditions may occur with resultant peat accumulation (Gastaldo & Staub, 1995). Hence, records of plant communities that grew under these climatic conditions often include peat mires, with a lower probability for preservation of macrofloral remains in other parts of the landscape due to low sediment yield. At the other climate extreme, available sediment may be higher where evaporation greatly exceeds precipitation, but rainfall may be extremely limited and temporally concentrated (rainfall less than four months of the year in warm climates; Cecil & Dulong, 2003). Under such climatic conditions, however, sediment transport is restricted to times of high-intensity rainfall with high erosive power. Even with little vegetative cover to bind sediments, sediment transport is limited by the lack of water to do the work, which diminishes potential for organic matter burial and preservation (see the effect of water table below). Under such arid and semi-arid conditions, taxonomic diversity and plant density per unit area are relatively low. Plant material may be preserved in unique settings, such as alkaline lakes, which may preserve aerial debris from small deciduous taxa that surrounded the site (e.g., Beraldi-Campesi et al., 2006), or gypcrete and/or calcrete soils, in which subterranean rooting structures may be preserved. But, such occurrences are rare and may be associated with a rapid influx of sediment (e.g., volcanoclastic ash-fall or higher-than-average rainfall resulting in fine clastic transport and deposition) and changing geochemical conditions. Hence, the probability of preserving plant material growing under extremely dry conditions is very low to insignificant, although such plant assemblages have been inferred from parts of the stratigraphic record (Retallack & Dilcher, 1988) and seasonally dry to arid communities have been reconstructed (e.g., Francis, 1984; Cantrill et al., 1995; Falcon-Lang & Scott, 2000; Falcon-Lang & Bashforth, 2004).

It would appear, then, that plant preservation in clastic rocks is promoted by equable climatic conditions, where precipitation equals or just exceeds evaporation and rainfall patterns are more seasonal in distribution (4–7 months/year), which would result in increased sediment load in streams and catchments (Cecil et al., 2003). The potential for plant-part preservation, though, still requires accommodation space for sediment burial and geochemical conditions that retard or prevent decomposition. Hence, it is more likely that a plant-fossil record will be generated within lacustrine, fluvial, tidal channel, and near-shore environments than in aerally exposed sites where pedogenesis and biomass recycling control the landscape (Gastaldo & Huc, 1992; Gastaldo, 2004).

In the broadest generalization, two sedimentological processes control the stratigraphic record in continental and marine environments, aggradational and degradational (erosional) processes, both of which are controlled by climate (Bull, 1991). As the concepts imply, aggradational sequences build up sediments in parts of a sedimentary basin, whereas degradational sequences remove sediments and redistribute them elsewhere within that or an adjacent basin. There is an interplay between both aggradation and degradation at various scales (within beds, architectural elements, channel-fill complexes, major depositional systems, etc.; Miall, 1990). Additionally, the record of each is influenced by autocyclic (e.g., channel migration) and allocyclic (e.g., tectonism, eustacy, climate) processes operating at any point in time and space (Beerbower, 1961, 1964; Demko & Gastaldo, 1996).

The highest probability for preservation of plant fossils exists within regional-scale aggradational sequences immediately above the contact with the previous regional-scale erosional event (Gastaldo, 2006). This point of transition between erosion and aggradation reflects a change in base level and the generation of increased accommodation space. Aggradational processes build up continental sequences via the transport and deposition of siliciclastics from an erosional source area. Sediment accumulation may occur in confined, intermontane basins within the source areas or further away, near local or regional base level. Pedogenesis may modify overbank sediments spread between the interfluvies (Retallack, 2001), and soil-forming processes generally are assisted by the presence of some type of vegetational cover, the composition of which is controlled by the prevailing climate (Ziegler et al., 2003) and the invertebrate fauna that utilizes this resource (Raymond et al., 2001). The level of the regional water table will control the geochemical pore-water properties at all depths, concomitantly impacting decay of buried organic matter. Preservation of buried plant detritus is most likely when the regional water table is persistently high over millennial or longer time scales, rather than when the water table fluctuates dramatically, permitting percolation of oxygenated rainwaters through soil and buried sediments (Gastaldo & Demko, 2005).

Base-level changes in transitional (coastal plain, deltaic, estuarine, and tidal flat) and nearshore marine (delta front, barrier island) settings may either be tectonic or eustatic in nature, or a combination of both of these allocyclic mechanisms operating over different time scales. Debate continues as to how to tease apart tectonic from eustatic effects within the stratigraphic record as the primary mechanism

controlling accommodation space for sediment burial (e.g., Klein, 1992; Christie-Blick & Driscoll, 1995; Miller et al., 1997). But, the fact remains that the long-term record of aggradational and degradational processes in coastal and marine depositional regimes may be controlled by eustacy (for this discussion, the short-term tectonic influences on generating accommodation and plant-part preservation will not be addressed; see Gastaldo et al., 2004a).

At certain scales of inquiry, paleoecology must consider the regional sedimentological framework within which ancient landscapes are preserved. The paradigm of sequence stratigraphy (Posamentier & Allen, 1999) provides a model that permits the effects of eustacy, climate, and tectonics to be integrated into a larger-scale framework. Eustatic cycles are based on the marine stratigraphic record and are asymmetrical over time, with rapid transgressive (onlap) sequences and prolonged regressive (offlap) sequences (Miall, 1990). Sequences are bounded above and below by unconformities, which often are exposed subaerial surfaces (identified by paleosols in terrestrial landscapes). Each onlap or offlap sequence is composed of parasequences, which are defined (van Wagoner et al., 1990) as a relatively conformable succession of genetically related beds bounded by marine flooding surfaces and their correlative updip (inland) surfaces (paleosols). Note that although the marine record may consist of a number of stacked parasequences, the continental record of these sea level changes may be locked within a single (thick) paleosol. Parasequence sedimentation occurs when accommodation is generated by a rapid rise or fall in sea level. Each change results in an asymmetrical, shallowing upward cycle somewhere within the basin but not everywhere coincidentally. Parasequences are stacked in various patterns across the basin over time. Transgressive systems tracts (TSTs) occur where successive parasequences overstep each other in a landward direction, and coastlines move over the continent, into more interior areas. When sea level has reached its maximum depth, the shoreline reverses its direction and progrades seaward, building up deposits of transitional and nearshore sediments in a series of parasequences within a highstand systems tract (HST). As sea level begins to fall, coastal progradation may continue until a time when the shoreline drops below the position of the previous shelf-slope break or one where the fall in relative sea level does change the position of the shoreline in the basin. The first situation results in the fluvial incisement (down-cutting) and erosion of former HST deposits, and transport and deposition of these mobilized sediments as lowstand systems tract (LST) turbidites in deep marine settings.

For the general purposes of this discussion on transitional environments, preservation of autochthonous and parautochthonous fossil plant assemblages occurs primarily when sea level is high, that is, within aggradational HST parasequences. It is in these settings where high sedimentation rates and high regional water tables prevail (characterized by inceptisol formation and wetland vegetation). When sea level drops and LST deposition takes place, degradational processes operate within the then-exposed HST deposits. All buried assemblages are subject to effects brought on by a lowering of regional water table coincident with the newly established, lower (oceanic) base level.

In summary, climate not only controls the distribution of vegetation across the landscape but also the timing and nature of sedimentation, within which plant parts are buried and potentially preserved. For these reasons, the plant fossil record in more proximal and, therefore, somewhat higher-elevation siliciclastic continental environments is biased toward low diversity, seasonal to humid, wetland communities in which geochemical conditions exist that may retard decay of plant debris. When these settings are subjected to sudden base-level change (e.g., tectonic coseismic subsidence), new accommodation space is generated and filled rapidly. This sedimentary infilling (aggradation) is accompanied by a rise in regional water table, removing some buried organic matter from the effects of oxygenated groundwater. If climate remains relatively humid during landscape stasis, groundwater level will remain high and buried organic matter can be preserved. But, if climate trends toward more seasonal and/or semi-arid to arid during landscape stasis, water tables will drop and decay of buried organics will occur. Entombed organics may be lost entirely from buried sedimentary sequences if sediments are not somewhat compacted, or may be reduced to impressions where some compaction has taken place in fine-grained sediments. Early diagenesis may promote mineralization of buried detritus, including pyritization, limonitization, and permineralization with calcite or silica.

Plant assemblages in coastal plain and transitional settings are also biased toward wetland communities growing under seasonal to humid climates. The reasons are similar to those provided above. Coastal and transitional communities already are at or within ca. 2 m of mean sea (base) level and grow within a progradational regime where sediments, in general, accumulate. Even in these basinal settings, preservation potential is high only when accommodation space for sediments is generated either by localized tectonic or compactional subsidence and concomitant sea-level rise, or eustatic rise in association with

transgression without ravinement (Liu & Gastaldo, 1992b). The latter situation commonly occurs within incised valleys where gradual sediment aggradation in a more proximal area, closer to the sediment source, allows for a thick sedimentary package in which plant fossils are preserved (Demko et al., 1998). Preservation potential is highest in subsequent parasequences during the phase of rapid aggradation, again, if the regional water table ascends as sediment accumulates and is maintained over the long term (fourth-to-third order cycle durations of 10^4 – 10^5 years). The fact that there is a bias toward an overrepresentation of wetland communities through geologic time, preserved within predictable settings by identifiable mechanisms, allows for their direct comparison under broadly isotaphonomic conditions.

Paleosols, biochemical, and geochemical proxies. Although now readily recognized and widely studied, it is hard to believe that until 25 years ago, paleosols were barely recognized in pre-Quaternary rocks. Paleopedology focuses on the soils that formed in past landscapes. Paleosol classification schemes may be based on modern soil-forming processes (Mack, 1997; Retallack, 2001b) or pedogenic processes that result in identifiable characters (Mack et al., 1993; James et al., 1998). The mosaic of soil types that exists across any landscape reflects the variation in physical and chemical features resulting from variations in climate and vegetation (Kraus, 1999). Soils may form in as little as a few hundred years (wetland entisol/inceptisol) or over several millennia (oxisol/spodosol), and well-developed soils usually define major unconformities in terrestrial stratigraphic sequences (e.g., Driese et al., 1994; Shanley & McCabe, 1994; Joeckel, 1995; Olszewski, 1996; Cecil et al., 2003; Demko et al., 2004). Evidence of colonization by plants and animals may include the presence of root traces or drab halos, where organic matter has been degraded and color differentiation enhanced by dehydration of ferric oxyhydrates during burial (Pfefferkorn & Fuchs, 1991; Retallack, 2001b), or ichnology (e.g., Hasiotis, 2003). Most often, though, organic matter is recycled through the soil system, leaving little or no physical evidence of the specific kinds of plants that biologically modified the sediment. Dispersed organics may remain within the soil profile, such as phytoliths (Strömberg, 2004), carpoliths (Thomasson, 1983), and meso- or micro-debris; some may be identifiable systematically, whereas others may be amorphous and unidentifiable. Regardless, many plant parts retain original biochemical information (Jahren et al., 2004b, 2006) that can be used for paleoecological restoration. In addition, such debris may act as the nucleating agent

for soil nodules or concretions (e.g., Pye et al., 1990), if bacterial activity and geochemical conditions permit.

By their nature, rooted-in-place, autochthonous assemblages allow correlation between paleosols and the plant community under which they developed. But, because in situ assemblages are a rarity, the source plants and vegetation under which the majority of paleosols formed remain unknown. In addition, long-exposed terrestrial surfaces can be subject to changing climatic and biotic agents resulting in compound soils affected by a number of potentially very different kinds of physical and biotic conditions. The question further arises as to possible relationships between specific soil types and specific kinds of vegetation (arborescent vs. herbaceous; gymnospermous vs. spore-producing), and whether diversification of vegetation types over the Phanerozoic has resulted in the diversification of soil types. Such questions are focused more on those soils that form under seasonally dry conditions, such as vertisols, alfisols, and spodosols (Cecil & DuLong, 2003; Driese et al., 2005). In contrast, very wet and very dry soils, at the ends of the climatic spectrum, present plants with a unique set of physical and physico-chemical conditions controlled by persistently high water tables (e.g., histosols, laterites), or high evapo-transpiration rates and very low rainfall (e.g., calcisols, gypsisols) that affect vegetational structure independently of its phylogenetic composition. Note the great similarities among Late Mississippian, Pennsylvanian and Permian, Late Cretaceous, and Neogene peat-accumulating histosols, despite the enormous differences in the phylogenetic composition of the vegetation under which they formed (it is not possible to compare the other end of the spectrum because of taphonomic constraints).

There is evidence of change in soil structure with the advent of arborescent (tree and shrub) growth forms, accompanied by the increasing depth of root penetration (Driese et al., 2000). During the Early to Middle Devonian (Elick et al., 1998), soil thicknesses and types were controlled more by illuviation and translocation (Driese & Foreman, 1992; Driese et al., 1992) than by organic degradation and soil respiration. Pre-vascular plant-soil types have been described (e.g., polsterland; Retallack, 1992), presumably formed under a bryophytic vegetation (Strother, 2000). Many of the Middle Devonian soils in which autochthonous assemblages are preserved are poorly developed wetland paleosols (e.g., Allen & Gastaldo, 2006; Greb et al., 2006), although Retallack (1997) infers better-drained and -forested alfisols from Antarctica during this time (but see Dahms et al., 1998). A wider range of soil types appears within

continental sequences during the expansion of gallery forests in the Late Devonian (Algeo & Scheckler, 1998). The subterranean plant parts preserved in these soils, if any (Pfefferkorn & Fuchs, 1991), are generally root traces, such as clay-filled voids (Retallack, 1999), rhizoliths (e.g., Schneider & Rossler, 1996; Kraus & Hasiotis, 2006), or rhizotubules and rhizocretions (Demko et al., 2004). Typically, the community structure responsible for origin of a paleosol is inferred by analogy with modern biomes (Retallack, 1992, 2001b). Such an approach is more consistent with angiosperm-dominated landscapes of the Tertiary (e.g., Retallack et al., 2001) than with ecosystems dominated by extinct gymnosperms and lower vascular plants.

Paleosol bulk-organic matter (OM) retains the carbon isotope ($\delta^{13}\text{C}$) signature of the contributing plant matter (Jobbágy & Jackson, 2000). Consequently, isotopes have been used as a proxy to recognize unique metabolic pathways (C_3 or C_4 grasslands; e.g., Fox & Koch, 2003, 2004; Pagani et al., 1999) and to characterize their relative proportions in parent vegetation. Isotopes also have been used to assess paleoclimate (e.g., Boom et al., 2002). Soil OM is derived from the decay of biomass produced under C_3 , C_4 , or Crassulacean acid metabolism (CAM) photosynthetic pathways. The C_3 and C_4 isotopic composition of carbon varies from -25‰ to -32‰ and -14‰ to -10‰ , respectively. Presently, there is no evidence that C_4 pathways existed prior to the Miocene, although inferences have been made about CAM (Raven & Spicer, 1996). This fractionation persists upward through the food chain, with incorporation of the isotopic signal into tooth enamel (e.g., Fox & Koch, 2003, 2004). However, the carbon isotopic signal in soils may be altered by decay processes (e.g., Bowen & Beerling, 2004), leading to the use of taxon-specific biomarkers (e.g., Lockheart et al., 1997) that, in the absence of recoverable fossil-plant debris, may make it possible to differentiate the contribution of specific taxa (Nguyen Tu et al., 2004; Smith & White, 2004).

Stable carbon and oxygen isotopes recovered from calcite cements within soil carbonates (concretions, nodules, amorphous masses) also provide paleobarometric data for the time at which calcite precipitated (Cerling, 1984, 1991). Pedogenic carbonates have been used as an indirect method to estimate the paleo-atmospheric CO_2 concentrations and climate, despite complexities for which analytic compensation must be made (Ehleringer & Cerling, 2002; Tabor et al., 2007), and several models have been developed (Cerling, 1991; Yapp & Poeths, 1996).

In the cases where pedogenic carbonates reflect the incorporation of atmospheric CO_2 , it is possible to

reconstruct paleoclimates and, in turn, paleoprecipitation regimes (e.g., Tabor & Montañez, 2002). There are numerous Tertiary-age examples based on multiple proxies (pedogenic carbonates and tooth enamel; e.g., Koch et al., 1995, 2003), with fewer further back in deeper time. Triassic climate, for example, generally has been interpreted as warm to semi-arid under monsoonal seasonality (e.g., Rees et al., 2002). Yet, Triassic macrofloral assemblages are interpreted to indicate the prevalence of warm, humid climates (Ash, 1999), probably reflecting the deposition of plant-bearing beds during wetter intervals within incised valley systems (Demko et al., 1998). Recently, Prochnow et al. (2006) acquired isotopic data from Triassic pedogenic carbonates. They estimated atmospheric CO₂ concentrations from the micritic fraction using the equations of Cerling (1999), and temperature using both oxygen and carbon isotopic values. They inferred a trend in the Early Triassic of the southwestern U.S.A. from arid to semi-arid (aridisols) conditions in the upper Moenkopi Formation to a more humid climate (alfisols) in the lower Chinle Formation, followed by a drying trend in the upper Chinle (semiarid aridisols and inceptisols). In this same lithologic sequence, there is an overall paucity of fossil plants, and those that do exist are concentrated within a pluvial interval, which is no surprise, given the taphonomic constraints on plant preservation (see earlier discussion). Hence, in those parts of the stratigraphic record where aridity and/or high seasonality is inferred from isotopic evidence, the absence of well-preserved megafloral assemblages is not unexpected, given the geochemical conditions.

The most comprehensive spatio-temporal insight into a fossilized terrestrial plant community comes from the integration of paleosol and (bio)geochemical data from rocks bearing autochthonous mega- and microfloral plant fossils (e.g., Gastaldo et al., 1998). It is most common, however, to encounter parautochthonous assemblages, which occur in association with, but not as part of, paleosols. Such assemblages may have little or nothing in temporal context with the paleosol(s) immediately beneath or above them within the section (Gastaldo et al., 1995b). Caution is advised particularly where there are incongruencies in paleoclimate indicators in successive beds, such as when megafloral assemblages occur in sequences with, but not actually within, calcisols or aridisols. Such paleosols form at that end of the climate spectrum where preservation of labile plant tissues is unlikely. Hence, only rarely can the presence of a well-preserved plant-fossil assemblage in such a rock sequence be used to interpret a dry or arid community.

Spatial patterns. Spatial relationships of taxa within the landscape are dictated by a variety of abiotic factors including edaphic (soil) conditions and topography, insolation, local water availability, and climate. Most landscapes are vegetational mosaics with taxa capable of growing anywhere conditions do not exceed the limits of their physiological tolerances (Beleya & Lancaster, 1999; Jackson, 2000). It is recognized that incumbency, competition, the role of light breaks, and other factors operate over the short term (10¹–10² years) to dictate the composition of any local community. But, in theory (e.g., Hubbell, 2001), over the longer term, all taxa within a species pool could be considered to be roughly equivalent and capable of growing anywhere within the region of the species pool or metacommunity (Law & Leibold, 2005), given the proper abiotic conditions. Hence, the composition of a plant-fossil deposit will depend on whether plant parts were shed physiologically (resulting in a lower fidelity record) or traumatically (resulting in a higher fidelity record), which plant parts were available at the time the deposit was formed, the chemistry of the depositional environment at the time, and the process-geometry of the sedimentary environment.

As a result of these factors, it is unlikely that most taxa in the immediate source vegetation will be represented within any given assemblage of fossil plants. Add to this fact the spatial scales of depositional environments, which are often orders of magnitude greater than what is exposed at most outcrops. It thus becomes clear that collections from a single hole-in-the-ground locality, less than 1 m² to several square meters, capture only a fraction of the forms that existed.

On the other hand, one must consider the regional metacommunity, broadly speaking, the regional species pool (Holyoak et al., 2005), that will contain many more species than any local site. This allows a solution to the limitations of small local samples, which is to make many small collections from across a sedimentary environment (e.g., Johnson & Ellis, 2002; Gastaldo et al., 2004b; DiMichele et al., 2007) or coeval stratigraphic horizon (e.g., Davies-Vollum & Wing, 1998). Statistically, such an approach will maximize the available information (Bennington, 2003), particularly where an autochthonous assemblage is sampled. This approach can be confounded by difficulties in tracing short-term time horizons over large spatial areas—the more finely one resolves time at a single outcrop exposure, the more difficult it can be to trace that time line laterally, without a well-defined and sedimentologically understood marker (such as an ashfall tuff). In addition, different times in geological history appear to have had different

landscape diversities, i.e., different metacommunity/species pool richnesses, even while retaining similar diversities on small, subhectare scales (Wing & DiMichele, 1995). This may involve a systematic time bias, such that Paleozoic species pools may be significantly less diverse than those of the Mesozoic and Cenozoic, leading to more uniformity among the best sampled sites along a gradient.

Sampling strategies. It is apparent that many interacting factors affect the genesis and maintenance of a fossil plant assemblage. In order to ensure maximum data recovery for paleoecological analyses, appropriate sampling strategies must be employed, dependent on the taphonomic signature of the assemblage, aerial extent of the exposure, both the lateral face and horizontal bedding surfaces, and degree of matrix lithification. Different techniques, for example, will need to be employed for autochthonous assemblages in well-lithified sediments, where standing vegetation and forest-floor litter are preserved in lithified mudstone (e.g., Taylor et al., 1992) versus those preserved in a non-lithified sediment in a semi-mummified state (e.g., Mosbrugger et al., 1994; Williams et al., 2003a, b). Similarly, lithified sediments preclude sieving and, thus, reduce the possibility of recovering small fruit and seed remains from parautochthonous assemblages, remains that would provide a more complete representation of the community than leaf or wood analyses alone (e.g., Gastaldo et al., 1998).

What's the question? Most macrofossil plant assemblages targeted for paleoecological analyses can be characterized broadly as parautochthonous. It is in these kinds of assemblages that the widest range of sampling strategies has been used. It is intuitive that the methods of sampling and analysis should fit the nature of the question (Magurran, 1998). One of the most significant questions regards the matter of biodiversity. One can ask legitimately what generates biodiversity, what does taxonomic richness reveal about ecosystem attributes and functions, and to what extent do rare species matter in comparative ecology? These have become subjects of considerable discussion in neoecology (e.g., Loreau et al., 2001; Ives & Carpenter, 2007). For example, Buzas and Culver (1999) demonstrated, using highly diverse assemblages of modern benthic foraminifera, that interregional differences (between the arctic and tropics, for example) in species richness can be accounted for mainly by the rare taxa that lie in the tails of species abundance curves, largely those known only once within huge numbers of samples (81% of the difference), very few of which have left a fossil record. Conversely, the top 10 dominant species in an

area (species pool) were found to have approximately similar distributions and relative abundances in each biogeographic region. Thus, if one is interested in ecological structure, it is likely that the dominant species in a local area, such as a hectare, will emerge quickly from small samples and most certainly if multiple samples are taken (e.g., Burnham, 1993b; Wing & DiMichele, 1995).

If comparisons are to be made across allochthonous assemblages, presence/absence data collection is most appropriate. If the objective is to determine richness (α diversity) of a local assemblage, for example, the focus should be on large numbers of specimens from within a given depositional environment, in order to maximize recovery of taxa; it is not necessary to laboriously collect data on debris cover (e.g., biomass estimate based on digitized area; Pryor & Gastaldo, 2000). Similarly, if the question concerns the proportionality of taxa with the intent of reconstructing community structure, which is the question of most paleoecological studies, it is generally appropriate to use a quantitative sampling method, the choice of which will depend on the taphonomy of the plant deposit, the nature of the plant fossils, and the nature of the geological exposure. In such studies, the objective most often is to understand vegetational structure, so that exhaustive sampling to detect a high proportion of the rare species is likely not necessary nor would the results justify the sampling effort required.

Quantitative sampling. Several different approaches to quantitative sampling have been employed in paleoecological studies of fossil plant deposits. (1) In studies of angiosperm-dominated floras preserved in fluvial and lacustrine settings, it is common practice to count leaves individually (Wing, 1984; Johnson, 1992; Burnham et al., 1992; Burnham, 1994; Gemmil & Johnson, 1997; Davies-Vollum & Wing, 1998; Wilf et al., 1998a), permitting direct conversion of leaf counts to biomass estimates, if desired (assuming size and leaf thickness to be approximately the same across taxa of a given life habit). (2) In permineralized peats (coal balls) of Pennsylvanian-age coal beds, square-centimeter (Phillips et al., 1977) or square-millimeter (Pryor, 1996) grids have been used to estimate taxonomic and organ numbers and biomass when overlaid on cut surfaces. When extensive bedding surfaces are accessible, (3) point count (Scott, 1977a, 1978, 1985) or (4) quadrat methods (Gastaldo et al., 2004b; DiMichele et al., 2007) have been employed. (5) For mine spoils or museum collections from a single depositional setting, rapid estimates of relative abundance can be made by the use of hand samples, treated as quadrats (Pfefferkorn et al. 1975; DiMichele

et al., 1991). These methods produce similar but not always identical results when applied to the same data sets. Wing and DiMichele (1995), for example, compared quadrat (frequency) methods and percentage representation (count) methods and found that the quadrat method systematically increases the abundance of rare taxa while reducing the abundance of common taxa.

Proportionality of taxa within an autochthonous or parautochthonous assemblage also can be assessed using subjective and/or semi-quantitative measures. Simple rank-order abundance (ordinal scale measure) is an attempt to assign a subjective representation to each taxon based on occurrence. Abundance classes most often are assigned on the basis of a visual estimate of the sample and ordered into abundant, common, and rare categories (Spicer, 1988). Kershaw (1973) noted that this scheme often underestimates small (fragmentary) taxa, and differentiation between the ranks can vary among individual observers. Adjustments of the method that impose a semi-quantitative approach include the modified scale of Braun-Blanquet (1932; Podani, 2006) and the Domin scale, which are based on an estimated percentage of cover for each taxon. These methods appear to be more robust and can be accomplished more rapidly when used in compression-impression macrofossil paleoecological analyses than estimates of cover using point counts (Spicer, 1988).

Autochthonous assemblages, those where stems and derived litter are preserved in situ, permit the most complete data collection. In such instances, it may be possible to evaluate the stature of individual plants, both herbaceous (Wing et al., 1993; Gastaldo et al., 2006) and woody (Williams et al., 2003a), including using mathematical estimates based on general studies of plant growth allometry (e.g., Niklas, 1994). Perhaps most importantly, such assemblages may permit evaluation of the density of individuals within the community, if the exposure allows, using both simple direct measurements and various means of calculating nearest-neighbor patterns (e.g., Wnuk & Pfefferkorn, 1984, 1987; Gastaldo, 1986; DiMichele & DeMaris, 1987; DiMichele & Nelson, 1989; Wing et al., 1993; DiMichele et al., 1996; Cúneo et al., 2003; Williams et al., 2003a, b). Such analyses can provide insight into vegetational structure in addition to the proportional taxonomic composition, which is the currency of most paleoecological analyses. In some cases, such as the Late Cretaceous flora found beneath an ash bed by Wing et al. (1993), it could be shown that species diversity and relative abundance were not correlated; angiosperms, although represented by the most species, did not account for the highest biomass in the assemblage, raising questions about

studies that assume a rough equivalence of taxonomic richness and ecological dominance. Biomass contribution from individual taxa also can be calculated in autochthonous assemblages, resulting in productivity estimates that can be compared with Recent communities (e.g., Williams et al., 2003b).

Spatial sampling. Spicer (1988) noted at the time that megafossil-assemblage sampling had been a somewhat haphazard process. He proposed a more codified set of strategies to be applied to bedding surface (two-dimensional) and volumetric (three-dimensional) samples. Several of these methods are effectively the same as neoecological sampling practices. These techniques can be supplemented by others, including bulk sieving of sediment and can provide additional data on the oft-overlooked meso- and micro-fossils (Eklund et al., 2004). The disarticulation of aerial plant parts is notorious for causing overrepresentation of some taxa and underrepresentation of others, relative to their proportional abundance in the parent vegetation (e.g., Burnham et al., 1992; DiMichele & Phillips, 1994). This means that various measures of taxon abundance in the fossil sample may be irrevocably biased, though correctable in some cases. The first step is to recognize that there rarely will be a 1:1 correlation between the quantitative composition of a parent vegetation and that of the derived fossil assemblage, whether autochthonous (Burnham et al., 1992; Burnham, 1997) or parautochthonous (e.g., oxbow lakes; Gastaldo et al., 1989).

For those quantitative studies that use quadrat-based methods, the size of the quadrat selected and the number of quadrats assessed are dependent on many factors, including logistical hurdles. The details of the sampling strategy will be dictated by the size and number of available outcrops, the degree of cementation and mineralization of the matrix, and the time and resources available to carry out the study (particularly if one is working under time constraints in a mine, or on another continent when the best localities are found at the end of a field season), meaning the choice is often less than ideal. In concept, the heterogeneity and scale of plant-part size have to be taken into account when selecting a suitable quadrat size. Spicer (1988) suggests a pilot study during which a pre-survey taxon/area curve (similar to a collection curve, see below) is developed to determine the minimum quadrat size for a specific assemblage. For example, it is most common for 0.5–1.0-m² quadrats to be evaluated at the outcrop scale where autochthonous leaf litter is concentrated, whereas assemblages in which large prostrate trees are preserved may be resolved more quickly and effectively by larger areas. Burnham (1989) further

developed guidelines for the choice of sampling strategies (few large samples vs. many small samples) based on the heterogeneity of the source vegetation, which can be approximated by a few simple on-outcrop tests.

Most recent studies of fossil plant assemblages consider explicitly the spatial aspect of the sample. Sample replicates, represented by two or more side-by-side samples, permit intra-site sample variability to be assessed and compared with among-site sample variability (e.g., DiMichele et al., 2007). Although such replicates are not samples from exactly the same site, they are as close as can be expected from fossil-field samples. Among-site comparisons require collections from multiple sampling sites (and replicates thereof) along a transect within a single sedimentary environment (e.g., Wing & DiMichele, 1995; Wilf et al., 1998a; Ellis et al., 2003; Gastaldo et al., 2004a; Willard et al., 2007). Transect studies of leaves preserved in modern sediments (Burnham et al., 1992; Burnham, 1993b) have demonstrated limits to leaf mixing in parautochthonous assemblages and, thus, suggest that most square-meter samples represent relatively local, at most half-hectare source areas, if the parent vegetation was a forest.

Data analysis. It is beyond the scope of this paper to discuss in detail the methods that can be applied to the analysis of various kinds of paleoecological data (see DiMichele & Wing, 1988). Data are often overanalyzed. It is frequently possible to grasp and describe major patterns accurately simply by inspection of the data. The techniques used to analyze patterns in modern vegetation usually can be applied equally well to fossil data. These techniques can be found in any number of general references, such as McCune and Grace (2002), and are widely available in many different computer software packages (including free shareware such as the R package, which includes manuals that offer various insights into the techniques and their peculiarities; R Project for Statistical Computing, 2007).

Most paleoecological analyses are searching for interpretable patterns in numerical data, often with an explicit spatial component. Data generally are stored in a matrix of samples by taxa. Sample similarities can be compared with a wide range of metrics, varying from those based on taxonomic presence-absence (e.g., the Jaccard coefficient), rank-order abundance (e.g., Spearman's rho), or ratio-scale quantitative measures of sample composition (e.g., Euclidean distance). These metrics are the basis for assessing sample similarities, although the choice of metric may be influenced by sample

size (Archer & Maples, 1987; Maples & Archer, 1988). The most commonly used exploratory multivariate method for the visualization of similarity among samples is ordination, and the most commonly used ordination methods at the present time are nonmetric multidimensional scaling (NMDS) and detrended correspondence analysis (DCA) (e.g., Miller et al., 2001; Holland, 2006; Willard et al., 2007). Data from other sources, such as the sedimentary environment, can be superimposed on these analyses. Classification methods, such as clustering, are used frequently in conjunction with exploratory methods (e.g., Liang, 2004). Hypothesis testing, regarding the existence of structure in the data, can be carried out with the use of such methods as analysis of similarity (ANOSIM). Methodologically similar to NMDS, ANOSIM examines variation in taxonomic compositional data within and between predefined samples. Discriminant function analysis is a hypothesis-testing classification method that employs a priori-defined groups to develop a classification algorithm that then can be used to assign unknowns to one of the existing groups with a specified degree of confidence.

Recently, several workers (e.g., Wing & Harrington, 2001: fig. 9) have plotted ordination first-axis sample scores against time to detect temporal patterns of change in similarity among samples. This is a powerful visual technique that can quickly reveal vegetational responses to environmental changes in time.

Spatial analyses of in situ vegetation may be reported in two (horizontal space) or three (horizontal space and vertical canopy height) dimensions (e.g., Wnuk & Pfefferkorn, 1987; Wing et al., 1993; Williams et al., 2003b; Gastaldo et al., 2004b). Additionally, the analysis may include various kinds of nearest-neighbor statistics to determine if plant distributions are random, ordered, or clumped (e.g., DiMichele et al., 1996; see Hayek & Buzas, 1997).

A final comment on method involves sample standardization. Under many circumstances, particularly when taxonomic richness is the objective of a study, it will be necessary to standardize sample size in order to reduce the biases of collecting intensity. This is generally accomplished with a method known as rarefaction (Raup, 1975). With this method, a distribution of samples of different sizes is created by repeated resampling from the original quantitative sample. This is done for each sample in the analysis. Then a standard sample size is chosen for the entire sample suite, drawn from the resampling curves created for each of the individual samples (for examples of the use of this method in plant paleoecology, see Wing & DiMichele, 1995, or Wilf et al., 2001).

RECONSTRUCTING THE PAST

Reconstruction of the past, in either visual or descriptive form, of individual species or of entire landscapes, is one of the major ways in which paleontologists make their work accessible, both to specialists and nonspecialists. Throughout the following discussion, a significant concern is the extent to which proportions of species are represented accurately in assemblage reconstructions. Of even greater concern is the degree to which the biologies of the individual plants are captured and integrated into the landscape reconstruction. The implicit dynamics of these past systems are in large part implicit in the portrayal of the reconstructed plants. The main fault of restorations, especially for those that purport to represent the pre-angiosperm world, is the implicit assumption that the plants can be analogized to extant angiosperms with life histories, growth habits, reproductive biologies, and stand characteristics that might be found in a local temperate woodland, so familiar to Northern Hemisphere scientists. This led Pfefferkorn (1995: 389) to label the paleobotanical community, on average, as “temperate climate chauvinists.” Take, for example, the ever-present uprooted lepidodendrid trees in Pennsylvanian wetland reconstructions, suggesting blowdown and uprooting as major disturbance elements in such assemblages. In fact, there is virtually no evidence ever reported for uprooting of these trees, or the tree-pit soil disturbances and tree gaps that accompany such events. Equally suspect are the many representations of dense, dark canopies in Carboniferous lepidodendrid forests, given that for many of the species the plants had no crowns until late in life. Such assumptions and analogies to modern vegetation are present to various degrees in reconstructions of the past from any time in geological history. Thus, it may be best to make clear statements about the assumptions regarding the plants and vegetation and, roughly, the confidence that can be placed in a particular reconstruction when offered for general consumption.

Disturbance and succession. The ecological dynamics of past communities, like those of today, are strongly influenced by disturbance and subsequent patterns of succession. Perhaps the most commonly studied disturbance agent is fire. An excellent review of the distribution of fire through time and its relationship to atmospheric oxygen levels is provided by Scott and Glasspool (2006). Wind disturbance, also common in the fossil record, is somewhat more difficult to document. Wnuk and Pfefferkorn (1987) documented a blowdown forest of Pennsylvanian age through access to large bedding surfaces exposed

in a coal mine and excellent sedimentological control. Flood disturbance has been documented for a variety of deposits throughout the fossil record (see citations below), the problem being the differentiation of flood disturbance from flood burial. Disturbance in volcanogenic landscapes has been described by Taggart and Cross (1980), Taggart et al. (1982), and Cross and Taggart (1982) in Miocene-age deposits and by Scott and Galtier (1985), as disturbance affected the evolution of early ferns, from the Mississippian of Europe.

Succession following disturbance is more difficult to document. Analyses of vegetational responses to fire need to be done at a finely resolved level, such as the study of Arens (1993), who analyzed a plant succession across a charcoal layer in Pennsylvanian-age deposits by taking small samples across the disturbance horizon. Pryor (1993, 1996) analyzed patterns of succession in a Pennsylvanian-age peat deposit using statistical patterns of plant co-occurrence in coal ball macrofossils. Also studying coal-ball permineralizations, Raymond (1988) analyzed succession during peat accumulation through patterns of successive root penetration. DiMichele and Phillips (1988) correlate patterns of plant response to disturbances within coal beds, again using macrofossils, by linking sedimentological features to recurrent assemblages. Many studies of coal palynology have revealed patterns of vegetational responses both to disturbance and to directional changes in the physical environment of the peat body through time of accumulation, generally related to hydrology and nutrient availability (e.g., Smith, 1962; Grady & Eble, 1990; Willard, 1993; Eble, 1999a, b; Figueiral et al., 1999).

Family portraits: Lots of plants but not much accuracy. Museums are populated by reconstructions of past worlds—dioramas and paintings and combinations thereof. These reconstructions of the past now can be found in abundance and readily on Internet websites, in textbooks, and in various popular venues. They generally are agglomerations of representative species from each of the main plant groups living at a particular time and in a particular region (for example, the wet tropics, a broad dry steppe, or a periglacial area). Such reconstructions often mix together plants from different sub-habitats, portray density unrealistically and, overall, can be terribly inaccurate as ecological depictions of the past. Add animals, at excessive densities and in unlikely combinations, and these reconstructions become little more than family portraits, time-averaged gatherings of extinct organisms.

Family portraits have their role, in that few places in the past are sufficiently well known or, if well known, are insufficiently diverse to make for a captivating reconstruction, one that passes along the sense of strangeness of a lost world. In their diversity, family portraits offer the viewer an abstract of the past. Thus, fossil family portraiture has its place and will not be displaced by reconstructions that aim at greater accuracy. Improvements could be made by paying more attention to autecology in particular.

Statistical reconstructions: Reconstructions based on the law of averages. More accurate representations of past vegetation have been based on data from actual paleoecological samples. Because most of such samples are from parautochthonous assemblages (see discussion above), the samples are representations of the original flora, subject to various kinds of taphonomic modifications. Thus, most paleoecological reconstructions based on data are based on some form of likelihood estimate, when the data are considered within the context of the various aspects of taphonomy. Such reconstructions may lack the representational breadth of family portraits, depending on the amount of the landscape they represent.

Statistical reconstructions often are based on the output of numerical analyses, particularly ordinations or cluster analyses of quantitative samples. Such samples provide a sense of recurrent taxonomic associations and may reveal gradients, outliers, and the patterns of relative commonness or rarity of particular combinations of taxa. In some instances, no actual image is produced from such analyses and the reconstruction is descriptive. Broadly considered, statistical reconstructions may also be derived from detailed sedimentological analyses in which plants are related to depositional environments and thence back to distribution on a larger landscape.

Examples of statistically reconstructed landscapes have grown in recent years. Some examples include schematic reconstructions based on various statistical summaries of data (e.g., DiMichele et al., 2002; Liang, 2004; Ricardi-Branco & Rösler, 2004), detailed artistic reconstructions based on quantitative analyses (LePage & Pfefferkorn, 2000; Falcon-Lang et al., 2001; Johnson & Raynolds, 2002; Willard et al., 2007), and descriptive reconstructions based on a variety of quantitative approaches and degrees of depth of statistical analyses of data (e.g., Spicer & Hill, 1979; Phillips & DiMichele, 1981; Raymond & Phillips, 1983; Wing, 1984; DiMichele et al., 1991; Pryor, 1996; Gemmill & Johnson, 1997; Wilf et al., 1998a; Figueiral et al., 1999; Howe & Cantrill, 2001; Johnson & Ellis, 2002; Spicer et al., 2002; Hofmann

& Zetter, 2005; Martín-Closas & Galtier, 2005; Wehrmann et al., 2005).

Johnson (1999) discusses in detail the procedures that went into the production of numerous reconstructed landscapes in the Prehistoric Journey exhibit of the Denver Museum of Nature and Science. These reconstructions are based on detailed field sampling of exposures and, thus, represent local views of much broader landscapes, not intended to be family portraits. Examples represented in this exhibit are illustrated in Johnson and Raynolds (2002) and include the Pennsylvanian-age Hamilton Quarry of Kansas (Rothwell & Mapes, 1988), the biota from the Late Cretaceous upper Hell Creek Formation of the northern Great Plains (Johnson et al., 2002), and the exceptionally high-diversity early Paleocene Castle Rock flora of Colorado (Johnson & Ellis, 2002; Ellis et al., 2003).

The Castle Rock flora demonstrates the fine line that separates a parautochthonous assemblage from an autochthonous assemblage. Preserved in a catastrophic flood, the Castle Rock flora is represented by a buried litter horizon with in situ tree trunks with roots in place in a subjacent paleosol. A later litter horizon (possibly derived from dying trees—compare with Burnham and Spicer [1986]) is preserved above the initial flood deposit (Ellis et al., 2003: fig. 4), buried by a second flood event. The abundance patterns of leaf distribution in transect samples and relative positions of disarticulated individual plants demonstrate minimal transport. Thus, this fossil deposit probably preserved regional spatial patterns and is similar to other stands of plants catastrophically buried by floods, where vegetation baffles sediment-laden water, inducing burial with minimal transport (e.g., Andrews et al., 1977; Allen & Gastaldo, 2006).

Direct reconstructions: Raising the dead. Possibly the most accurate reconstructions of past landscapes come from sites that were buried catastrophically by air-fall or waterborne volcanic ash, sediment carried by flood waters, often associated with low areas created by seismic activity, or by the encapsulation of vegetation by precipitation of minerals. The reconstruction of such vegetation is done, essentially, by raising the flattened vegetation backup, hence the label as “direct.”

Burnham and Spicer (1986) described vegetation buried by and preserved by volcanic ashfall near El Chichón volcano in Mexico—an initial burial of the forest-floor litter, ground-cover plants, and bases of trees, with a second layer of leaves preserved above the initial bed, representing the leaves from the standing forest, live at the time of the ashfall. A similar deposit was reported by Wing et al. (1993)

from Big Cedar Ridge, Late Cretaceous of Wyoming, buried by air-fall volcanic ash. In situ preservation of the vegetation revealed that ferns were the dominant major group, whereas angiosperms were the most diverse at the species level, demonstrating that diversity within higher taxonomic groups is not necessarily an indicator of dominance of that group, measured as biomass. Other examples of in situ floras buried by ash have been described by Wagner (1989) from the late Pennsylvanian of Spain, and Pfefferkorn and Jun (2007) from the Early Permian of China, in each case preserving plant stems and litter and allowing spatial and whole-plant reconstructions.

Catastrophic burial by flood-borne sediments often is associated with seismically induced changes in elevation, such as those accompanying the formation of Reelfoot Lake, Missouri, and the burial of the forest growing on that site (Penick, 1981). In rapidly subsiding basins proximate to sediment source areas, forests may be buried autochthonously in multiple, closely spaced layers (Gastaldo et al., 2004a), and even in tectonically less active areas, seismic activity may be essential for the creation of accommodation space and the in-place burial of forests (DiMichele et al., 2007). Autochthonous vegetation buried by flood-borne sediment can be found throughout the fossil record of terrestrial plants. Examples include the Devonian Trout Valley flora of Maine (Andrews et al., 1977; Allen & Gastaldo, 2006), numerous cases of Carboniferous lowland, wetland tropical vegetation (Gastaldo, 1992b; DiMichele & DeMaris, 1987; DiMichele & Nelson, 1989; DiMichele et al., 1996; Gastaldo et al., 2004b; Calder et al., 2006), high-latitude forests from the Permian (Taylor et al., 1992), Triassic (Cúneo et al., 2003) and Cretaceous (Falcon-Lang et al., 2001) cycadeoid stands (Wieland, 1916), and in situ fern thickets (Cantrill, 1996) of Cretaceous age, and younger vegetation, such as that of the Castle Rock flora mentioned above (Ellis et al., 2003). In all of these instances, T_0 spatial aspects of the original vegetation are preserved.

The most unusual way to preserve vegetation is by entombment in mineral matter precipitated around the standing plants. The best example of this kind of preservation is the Devonian Rhynie Chert, preserved in travertine deposits from mineral-laden hot springs (Rice et al., 2002). The anatomical preservation of the plants and animals in this deposit is spectacular. In addition, different assemblages of species, plant associations in particular sedimentary environments, and successional patterns have all been identified in what amounts to one of the most completely reconstructed fossil ecosystems.

Autochthonously preserved plant deposits will have their greatest impact when many are known, espe-

cially at multiple stratigraphic horizons in close succession, and before and after major extinction boundaries. This is an area in need of much more attention, and in which the gradual accrual of data will eventually provide a richer array of data points for comparison.

PALEOBIOGEOGRAPHY

Paleobiogeography is an increasingly important component of paleoecology. Such studies of plants were among the biological patterns that lent strong support to the idea of continental drift, prior to the widespread acceptance of plate tectonics (see Chaloner [1959] for review), and, later, helped refine study of continental positions (e.g., Ziegler et al., 1996; Berthelin et al., 2003). Vegetational studies also are of importance in the ground-truthing of climatic models (e.g., Wing & Greenwood, 1993; Upchurch et al., 1999; Beerling & Woodward, 2001; Rees et al., 2002; Poulson et al., 2007). The resolution of paleobiogeographic studies is, of course, much better in younger rocks, something paralleled by paleogeographic reconstructions. Furthermore, although basic patterns were apparent in some of the earliest studies, the degree of resolution has improved significantly through time, with improved taxonomies and better paleogeographies.

Paleozoic. The Paleozoic is characterized by a combination of major evolutionary changes in plants, major changes in the relative positions of continental landmasses, high levels of variation in atmospheric composition and global climate, and great variation in sampling intensity at different times and places (DiMichele & Hook, 1992). Consequently, from the Silurian to the end of the Permian there really was a series of worlds in which plant distributional patterns were changing, sometimes dramatically, through time. There also are time intervals of considerable uncertainty due to poor sampling, intercalated among times of rich sample density during which subtle patterns can be detected (e.g., Edwards, 1990; Laveine et al., 2000). Through most of the later Paleozoic, continental landmasses were gradually coalescing into the Pangean supercontinent, resulting in many land-based connections permitting plant dispersal across wide areas. Thus, for the Silurian and Devonian and certainly for the later Carboniferous and Permian, it has been traditional to subdivide the world into large-scale floristic realms. Sampling evidence has consistently pointed to differentiation of three distinct regions: equatorial/low latitude, and north and south temperate high latitude (e.g., Chaloner & Lacey, 1973; Chaloner &

Meyen, 1973; Wnuk, 1996). Ziegler and colleagues (Ziegler et al., 1981; Rowley et al., 1985) added the element of climatic zonation, differentiating floristic provinces. Later, Ziegler (1990) and Rees et al. (1999, 2002) took an explicitly climate-based approach, recognizing ancient biomes as climatically bounded vegetational units, paralleling vegetational distribution on the modern earth (Walter, 1985). Ziegler et al. (2003) argue persuasively that atmospheric circulation patterns are the major controls on vegetational distribution, with due regard for the effects of elevation and paleogeographic locations of moisture sources (e.g., Ziegler et al., 1997).

Summaries of Silurian and Devonian paleobiogeography, the most problematic of the Paleozoic, can be found in Raymond et al. (1985, 2006), Raymond (1987), Edwards (1990), and Raymond and Metz (1995); these analyses suggest some largely latitudinal floristic differentiation with limited taxonomic overlap between regions. The much greater abundance of fossil plant collecting sites from the Carboniferous yields a more detailed understanding of phytogeography at that time. General summaries for the Mississippian include van Der Zwan et al. (1985), Raymond (1985), Raymond et al. (1985), Scott and Galtier (1996), and Raymond (1997). Iannuzzi and Pfefferkorn (2002) recently presented a case for a previously unrecognized warm-temperate floral belt in the late Mississippian of the paleo-Southern Hemisphere, demonstrating the continuing need for field sampling and refinements of the systematic framework on which these floristic analyses rest.

For the Pennsylvanian and Permian periods, there are a relatively large number of analyses of plant distributions, including some on fine spatial scales. The classic papers are those of Chaloner and Lacey (1973) and Chaloner and Meyen (1973), which argue for the progressive differentiation of floristic regions throughout the later Paleozoic, from one to three to five. Thirty years later, Rees et al. (1999, 2002) and Ziegler et al. (2003) had subdivided the late Paleozoic world more finely and demonstrated considerable similarity to patterns in the modern world. Fine-scale refinements of these broader patterns include those of Laveine and colleagues for the Pennsylvanian (Laveine et al., 1989, 1993, 2000; Laveine, 1997). These authors tracked the migration patterns of pteridosperms across the tropics and suggested significant geographic rearrangements of the positions of micro-continental landmasses in the eastern Tethys. Similarly, for the Permian, LePage et al. (2003) have demonstrated yet-to-be-understood physical connections permitting overlap of north temperate Angaran floral elements with those more typical of Euramerican equatorial regions, though principally extrabas-

inal equatorial elements. Broutin and colleagues (Broutin et al., 1995, 1998; Fluteau et al., 2001; Berthelin et al., 2004; Broutin & Berthelin, 2005) have demonstrated complex mixing of floras along the margin of the tropical regions, bringing together floras from western and eastern portions of the tropical belt with those from more southerly temperate regions. Cuneo (1996) and Iannuzzi and Rösler (2000) have examined phytogeographic patterns in the Southern Hemisphere during the Permian. Pant (1996) summarized paleophytogeographic patterns in India during the late Paleozoic. Li and Wu (1996) examine such patterns in China, and Oshurkova (1996) compares north-temperate Angaran and equatorial Euramerican floristic trends.

Mesozoic. During the Mesozoic, plants recovered from the major ecological disruption at the Permo-Triassic boundary, the Earth's climates were warm, at times from equator to pole, large animals dominated the herbivorous fauna for much of the time, and the angiosperms began to diversify and dominate some ecosystems. Consequently, as with the Paleozoic, many factors impinged on plant distribution and a simple summary of plant paleobiogeography during this time is not really possible.

During the Early Triassic, low latitudes and low-elevational areas of the Earth appear to have been dramatically altered, probably in terms of their biogeochemical cycles, to such a degree that fossil floras are rare. There certainly were extinctions at or near the Permo-Triassic boundary, the extent of which, however, is poorly understood. Despite claims of devastation (e.g., Retallack et al., 1996), it is clear that most major plant clades survived and vegetation was well along in the process of recovering by the Middle Triassic (Looy et al., 1999; Kerp et al., 2006). Ziegler et al. (1993, 2003) summarize some of the physical and biotic changes that occurred during the Triassic.

The Jurassic appears to have been a time of relatively long-term climatic uniformity over much of the globe, following a period of global warming at the Triassic-Jurassic boundary (McElwain et al., 1999). By tying climatically sensitive sediments (especially coals and evaporitic rocks) to the distribution of plants, Rees et al. (2000) concluded that maximum plant productivity during the Jurassic was concentrated in the midlatitudes, where the diversity of plant major groups also was highest. The tropics, in contrast, were dry and supported little if any rainforest vegetation; rather, such areas were populated by xeromorphic conifers and cycadophytes. Polar regions tended to be dominated by deciduous conifers and ginkgophytes. They further conclude that there were five major biomes that remained latitudinally stable

throughout the period, moving across the continental landmasses as the positions of the continents changed. Plant diversity followed the patterns of maximum climatic equability, being highest in the midlatitudes, dropping off toward the equator and poles (Rees et al., 2004); these authors also note a discrepancy between the distribution of plant and dinosaur fossils, which they attribute to taphonomic factors and argue that dinosaurs were most abundant in dry, savannah-like habitats rather than forests. Skog (2001) considered the biogeographic patterns of evolution of leptosporangiate ferns during the Mesozoic and found that most are known from and may have evolved in the midlatitudes or higher, associated with moisture availability.

The Cretaceous has been studied extensively by climate modelers. Some paleobotanical studies that have addressed Cretaceous climate, including plant-climate feedbacks, include those from Spicer et al. (1994, 1996), Upchurch et al. (1998, 1999), DeConto et al. (1999), and Beerling and Woodward (2001). Cretaceous plant productivity and biodiversity were broadly similar to those of the Jurassic in being highest at midlatitudes, where climates were most favorable (Spicer et al., 1993). However, there may have been high levels of terrestrial productivity in some areas of the tropics if continental and atmospheric circulation patterns favored high rainfall, given the climate-biome models of Upchurch et al. (1999). Certainly, peat accumulated at midlatitudes in western North America (Ziegler et al., 1987). Climate changes just prior to the end of the Cretaceous, particularly global warming, have been suggested.

Cenozoic. By the Cenozoic, the amount of geographic and elevational coverage preserved in the fossil record is so much greater than that known or preserved in the Mesozoic or Paleozoic that patterns of plant distribution can be evaluated at a much higher level of detail than in deeper time. For example, Manchester (1999) provides a broad review of North American Tertiary floras, noting a long and well-documented record of floristic exchange among the major Northern Hemisphere continents during this time interval. Similarly, Jacobs et al. (1999) follow the history of grass-dominated ecosystems during the Cenozoic, lending support to a complex history prior to appearance of extensive grasslands in the Miocene. Retallack (2001c) has also reviewed the origin and spread of grass-dominated ecosystems and argues that the long-term co-evolution of grasses and grazers may have contributed significantly to cooling, drying, and climatic instability. The most recent studies of the origin of grasslands have used phytolith evidence (Strömberg, 2002, 2004, 2005) and suggested that

the evolutionary radiation of grasses and grazers was decoupled. Prasad et al. (2005), through the examination of grass phytoliths in dinosaur coprolites, were able to determine that grasses were present in significant enough numbers during the Cretaceous to be a food source for dinosaurs. Burnham and Graham (1999) were able to examine the pattern of Neotropical rainforest species composition and turnover from the Miocene to the Recent by a combination of paleobotanical and neobotanical data. They show that plant migrations did not follow those of animals after the formation of the Panamanian isthmus three million years ago; rather, the southern forests have remained relatively free from major, ecologically disruptive invasions. In addition to larger-scale biogeographic studies, it is possible to detect elevational controls on vegetation in Tertiary-period deposits because of the preservation of basins at higher elevations, typically eroded in deeper time (e.g., Taggart et al., 1982; Wehr & Manchester, 1996). The point of these examples is to demonstrate the high degree of spatial and temporal resolution that can be achieved in the study of the biogeography of Cenozoic floras and major plant lineages, to a degree not comparable in deeper time. In contrast to this generality, Collinson (2001) notes that the Cenozoic ferns, although often well known and with distributions exceeding those of their extant descendants, are in some cases more poorly known than ferns from the Mesozoic and Paleozoic, in large part because they are less abundant elements of Cenozoic vegetation than ferns from these earlier times.

APPLIED PALEOECOLOGY

The obvious applications for paleoecological data sets are in the assessment of spatial (within time units at the resolution of age or stratigraphic sequence) and temporal (across time at the resolution of epoch or period) patterns from which (1) communities and ecosystem structure can be evaluated (e.g., Taylor et al., 1992; Wing et al., 1993; Mosbrugger et al., 1994; Falcon-Lang & Cantrill, 2002; Gastaldo et al., 2004b; Falcon-Lang & Bashforth, 2004, 2005; Falcon-Lang, 2006; DiMichele et al., 2007); (2) governing principles of stasis, turnover/replacement, and extinction and assembly laws can be tested (e.g., Knoll et al., 1984; Wolfe & Upchurch, 1986; Pfefferkorn et al., 2000; DiMichele et al., 2001b, 2002, 2004; Willard et al., 2007); and (3) phytogeographic realms can be delimited (e.g., Raymond, 1985; Raymond et al., 1985; Spicer et al., 1993; Rees et al., 2000, 2002; Rees, 2002). Because plant communities are non-mobile, they reflect the unique climatic conditions

governing growth, reproduction, and dispersal across the landscape. Hence, the suite of plant organs, from which the community and/or ecosystem was reconstructed, is a proxy for the paleoclimatic conditions under which the parent plants lived.

LEAVES AND LIVING RELATIVES AS PALEOCLIMATE PROXIES

Nearly a century ago, Bailey and Sinnott (1915, 1916) recognized that leaf morphology could be used as a proxy for climatic conditions, and paleoclimate estimation protocols have long been in the refinement stage. Two principal approaches to climate estimation have arisen (but see also Uhl & Mosbrugger, 1999) based on the morphology of angiosperm fossil-leaf assemblages: leaf margin analysis (LMA; Wolfe, 1979; Wing & Greenwood, 1993; Wilf, 1997) and climate leaf analysis multivariate program (CLAMP; Wolfe, 1993). LMA correlates mean annual temperature (MAT) with the proportion of woody dicot species in a flora having entire (non-toothed) leaf margins. CLAMP takes a multivariate (canonical correlation) approach, involving 31 leaf morphological characters and 11 climate variables (e.g., Spicer et al., 2004, 2005). LMA is faster and simpler to use, but CLAMP offers the computation of a number of different climate variables including MAT, mean cold and warm month temperature, and mean annual precipitation (MAP), and offers the opportunity for additional statistical and graphical manipulations (Green, 2006). For comparison of methods, see recent papers by Jacobs (2002) and Uhl et al. (2007). MAP has been somewhat more difficult to estimate from leaves, and leaf-size analysis has been investigated as a simple and straightforward method to obtain such estimates (Wilf et al., 1998b, 1999).

Proponents for both climate-estimation models continue to test the validity, constraints, and controls on foliar physiognomic responses, often with disparate results when evaluating the same flora (e.g., Wiemann et al., 1998; Gregory-Wodzicki, 2000). With a bias toward preservation within wetlands, Kowalski and Dilcher (2003) found that living dicot communities growing in these North American settings have a higher proportion of toothed leaves that resulted in an underestimation of inferred paleotemperatures ranging between 2.5°C and 10.0°C, regardless of methodological approach. To redress the underestimate, they introduced wet-site regression equations and proposed that predictive equations be redeveloped using sites more analogous with those identified in deep time. Depending on the biome under consideration, both overestimates (e.g., Jacobs, 2002) and underestimates (e.g., Greenwood, 2005) of climate parameters have been reported, with underestimation the result of low-

diversity angiosperm floras. But, when high species diversity exists, such as in the paratropics and tropics, there may be a minimum number of taxa above which credible MAT estimates and somewhat less credible MAP estimates can be made. Burnham et al. (2005) found a correlation between species richness and the accuracy of climate estimates in the Neotropics; estimates came within $\pm 2^\circ\text{C}$ of recorded temperatures when 50% of the highest rank-ordered taxa were used. More accurate estimates were achieved as the taxonomic number increased. When less than 25 taxa were used in an analysis, estimates were outside the accepted $\pm 2^\circ\text{C}$ margin of error (Wilf, 1997). In their data, a bias toward serrated leaves existed in the data set (comprised of the top 10 rank-order taxa), with this bias disappearing once the top 20 taxa were taken into consideration. Hence, Burnham et al. (2005) concluded that habitat may not be relevant to the bias associated with MAT estimates. Additionally, they found that MAP estimates for all their sites were too low, even when all taxa were used.

The other approach to climate reconstruction is the nearest living relative (NLR; Mosbrugger, 1999) model, where the climatic requirements of the NLR of a fossil taxon is, or assemblage components are, used to estimate the paleoclimate under which the organism(s) lived. Mosbrugger and Utescher (1997) introduced a variation, the coexistence approach (CoA), in which the climate requirements of a fossil assemblage are estimated by using a compilation of the ranges of climatic requirements of each taxon's systematically NLR. Climatic variables (MAT, MAP, etc.) under which all taxa within the assemblage could have grown together are used to develop the estimates. Theoretically, this method can be applied to assemblages where at least one NLR can be identified, but, obviously, resolution increases with an increase in the number of taxa in an assemblage with NLRs. Mosbrugger and Utescher (1997) demonstrate a strong congruence between climate parameters in both Recent and Neogene floras (88%–100% of coexisting taxa). Tests of the CoA against both LMA (Uhl et al., 2003) and CLAMP (Utescher et al., 2000; Liang et al., 2003) demonstrate its applicability to Tertiary assemblages. When compared with LMA, both approaches can produce sensible and consistent results, depending on the flora (e.g., Liang et al., 2003), when the standard error of the leaf-physiognomy paleoclimate data is taken into account. But Uhl et al. (2003) caution that reconstructions based on leaf physiognomy are influenced by factors not related to climate, such as sample size and taphonomy. When results are compared between CLAMP and CoA analyses, lower paleoclimate estimates were calculated using CLAMP for European Mio-Pliocene

assemblages (Mosbrugger & Utescher, 1997; Utescher et al., 2000) and for a Miocene assemblage preserved in diatomaceous lake shales in Asia (Liang et al., 2003). A similar CLAMP underestimate is reported for the Shanwang site when compared with LMA (Sun et al., 2002b).

This begs the question as to whether or not such protocols can be applied to the non-angiosperm world. Most non-angiosperm deciduous taxa have no NLRs. Thus, to date, climate estimates based on such taxa have met with only partial success. In the deepest time analysis to attempt LMA, Glasspool et al. (2004) evaluated Permian-age Cathaysian gigantopterids, which have angiosperm-like broad leaves; the results of the analysis are limited, however, by lack of another independent proxy for temperature. Another taxon, *Ginkgo* L., is interpreted to have had similar ecological distribution since the Mesozoic in disturbed stream-side and levee environments (Royer et al., 2003). The ecological constraints of Late Paleozoic representatives (*Dicranophyllum* Grand'Eury) are still uncertain; the taxon has been found associated with Lower Permian Southern Hemisphere coals (Guerra-Sommer & Cazzulo-Klepzig, 2000). And, because living *Ginkgo* is monospecific (*G. biloba* L.) and there are no unequivocal natural stands today (unlike the recently discovered Wollemi Pine, Araucariaceae; Chambers et al., 1998), there is a high probability that Ginkgoaleans were adapted widely to a variety of habitats (see Rees et al., 2002). On the other hand, stomatal trends of fossil *Ginkgo* are believed to parallel those of the living taxon grown under varying atmospheric gas concentrations (Beerling & Royer, 2002a; see below).

Due to the seeming obstacle of ecological homology, other workers have utilized permineralized wood assemblages to estimate paleoclimatic parameters (e.g., Chaloner & Creber, 1990). Recently, though, Falcon-Lang (2005a) and Poole and van Bergen (2006) have demonstrated that the relationship between climate and growth-ring parameters in modern trees, in part, invalidates the use of fossil woods as climate proxies. This is due to unconstrained variability in tree response to climate-forcing (i.e., growing-season length and growth conditions, seasonality, productivity) on a global scale, applicable to both angiospermous and coniferous woods (Falcon-Lang, 2005a, b).

Proxy approaches to understanding ancient ecosystems and the environmental conditions of their formation at whole-system levels have been applied extensively to such settings as peat-forming environments, where physical controls and taphonomy often are considered to be conservative and independent of plant composition. There is an extensive literature

on peat-to-coal models, including environmental inferences. Models, such as those of Diessel (1986) and coworkers, that would identify modern vegetational equivalents, such as reed-dominated versus woody forest-dominated systems, in Carboniferous forests based on coal macerals do not take into consideration the significant differences in the plants from different times in geological history and, thus, risk inappropriate ecological conclusions. As pointed out by Collinson and Scott (1987) in a comparison of Carboniferous lycopsid-dominated systems with Cretaceous to Recent taxodiaceous-dominated systems and DiMichele and Phillips (1994) in an examination of Carboniferous systems, the qualities of the plants cannot be ignored.

STOMATAL DENSITIES AS CLIMATE INDICATORS

The developmental response of leaves to elevated pCO_2 as reflected in leaf stomatal density has garnered great attention over the past decade (e.g., McElwain & Chaloner, 1996). Application and limitations of the approach have been reviewed elsewhere (e.g., McElwain, 1998; Royer, 2001; Beerling & Royer, 2002a; Roth-Nebelsick, 2005), and the reader is directed to these contributions. An inverse relationship exists between the pCO_2 and stomatal index (SI; Poole & Kürschner, 1999) such that stomatal indices (the ratio of stomata to epidermal cells) decrease as the concentration of atmospheric CO_2 increases. This inverse response is found in both angiosperms and gymnosperms (e.g., Kouwenberg et al., 2003) but is not limitless. It has been demonstrated in modern angiosperms that not only will different species within the same genus reach their own SI limit at different pCO_2 (e.g., *Quercus* L.; Kürschner, 1997), but species of the same genus (*Quercus*) grown under identical climate and atmospheric gas conditions exhibit statistically significant differences in both stomatal density and SI values (Cantor et al., 2006). Hence, caution is necessary when using this approach in deep time (Kürschner, 1997).

There have been attempts to apply non-angiosperm stomatal indices in other parts of the pre-angiosperm record. For example, a number of researchers have used the Ginkgoales to examine geological trends in pCO_2 . Retallack (2002) used extant *Ginkgo biloba*, in part, to calibrate responses of fossil *Ginkgo* species back into the Late Triassic, and extended this even further back into the Permian, using pteridosperm taxa with purported evolutionary affinities to the Ginkgoales. The assumption, of course, is that all these related species exhibited the same physiological and developmental responses (Beerling et al., 1998) at

all times and places. Chen et al. (2001) examined modern *G. biloba* and found significant differences in stomatal patterns relative to timing of leaf maturation, leaf development, placement on short versus long shoots, canopy position, and sexuality. They concluded that only mature leaves of *G. biloba* should be used in any analysis. They (Chen et al., 2001) then matched stomatal estimates of $p\text{CO}_2$ from four extinct species of *Ginkgo*, ranging in age from Early Jurassic to Early Cretaceous, to the $p\text{CO}_2$ curve of Berner (1998) and found congruence for only two. NLRs for Jurassic cycadales also have been used (e.g., McElwain et al., 1999). Using stable carbon-isotope data, Beerling (2002) extended the approach to Carboniferous arborescent lycopods using extant tropical *Lycopodium cernuum* L. for calibration purposes, although acknowledging closer affinity to extant *Isoetes* L. Values derived from the stomatal indices of Carboniferous arborescent lycopods were consistent with the independent indicators of a drop in atmospheric $p\text{CO}_2$ concentration during the Late Paleozoic glaciation.

In the absence of one or more NLRs, McElwain and Chaloner (1995) chose to use nearest living equivalents (NLEs), defined by them as Recent taxa that grow in a comparable ecological setting and/or are structurally similar, in their evaluation of Devonian (*Juncus* L. = *Sawdonia* Hueber and *Aglaophyton* D. S. Edwards; *Psilotum* Sw. = *Aglaophyton*) and Carboniferous (*Araucaria* Juss. = *Swilingtonia* A. C. Scott & Chaloner and *Lebachia* Florin) plants. They found a marked contrast in all stomatal parameters between the extant and the extinct taxa. The Devonian fossil taxa exhibited significantly higher SI values than their NLEs, whereas values for the Carboniferous taxa plotted within the range of extant araucarians. These results were consistent with Berner's (1991) GEOCARB model, confirming a massive atmospheric drop in CO_2 from the Early Devonian through the Permo-Carboniferous. Again, using the NLE approach, with ginkgoaleans and cycadales, McElwain et al. (1999) linked major species turnover at the Triassic–Jurassic boundary to a 3°C – 4°C increase in global temperature.

For deep-time taxa without either an NLR or NLE, physiological and developmental responses have been inferred using even more generalized assumptions about stomatal responses. For example, Hesselbo et al. (2003) used the stomatal densities (SD) instead of SI values in plants from a Middle Jurassic sequence of Yorkshire to develop a general pattern. Although SI is more reliable than SD (Poole & Kurschner, 1999; Royer, 2001; Beerling & Royer, 2002b), preservational problems dictated use of the latter. Stomata patterns in pre-Mesozoic gymnosperms also

have been used to develop proxies for $p\text{CO}_2$. Cleal et al. (1999) evaluated stomatal parameters in the pteridosperm *Neuropteris ovata* Hoffmann across the Moscovian–Kasimovian (Wesphalian–Stephanian) boundary. Their results suggest an increase in atmospheric CO_2 in the very early Kasimovian, consistent with changes in vegetational composition and carbon sequestration (DiMichele & Phillips, 1996; Cleal & Thomas, 2005). More recently, Wang and Chen (2001) extended the application to the extinct arborescent lycopods, using cuticles recovered from leaf cushions and distal sporophyll laminae. The shift in values across the Upper Permian of China, tied to a shift in lithofacies, is attributed to a change in the physiological response of these taxa from C_3 to CAM photosynthetic pathways in response to an increasingly dry climate.

INFERRING PHYSIOLOGICAL RESPONSES OF EXTINCT PLANTS AND THEIR IMPLICATIONS

Paleobotanists are increasingly finding ways to estimate plant physiological functions and responses to environmental conditions. Konrad et al. (2006) developed a model to evaluate photosynthetic capability as it relates to diffusion resistance of the epidermal cells based on the size and depth of stomatal pores and mesophyll parameters (e.g., intercellular air space, mesophyll-cell area, and membrane resistances). They also added functions to evaluate the relationship between assimilation and temperature. The model permits use of stomatal morphologies and densities to calculate past CO_2 . Similarly, Royer and Wilf (2006) have proposed and evaluated a gas-exchange hypothesis that explains the relationship between leaf-margin morphology and climate variables. They tested the efficacy of the model, found that it accurately predicted the response of leaves from colder climates, and found an increased efficiency in transpiration and photosynthate production early in the growing season in taxa with toothed margins versus those with entire margins (this also may explain the higher proportion of toothed-leaved taxa in stressed wetlands). Additionally, plant response is enhanced at higher-temperate latitudes (38.8°N , colder temperate Pennsylvania; 35.7°N , warmer temperate North Carolina) where the plants maximize carbon gain when temperature is limiting but moisture and nutrient availability are not. They have concluded that the increased physiological functioning associated with serrated leaf margins may provide a proportionally increasing selective advantage with decreasing temperature (or water stress). This is reflected in empirical correlations used for paleo-temperature estimation. Another recent

hypothesis relating toothed-leaf margins to temperate climates is that of Feild et al. (2005), who suggest that teeth act as points of guttation, a process of relieving flooding of leaf tissues by root pressure on the vascular system. These authors propose that by relieving the negative effects of flooding, guttation permits root pressure to drive leaf developmental expansion. Cool, high-humidity spring weather, combined with moist soils in many temperate regions, would be conditions in which guttation was favored. In addition, this model explains the overabundance of toothed-margin leaves in wet habitats (Burnham et al., 2001; Kowalski & Dilcher, 2003). In contrast to these organ-scale studies, Beerling and Osborne (2002), working at the level of the biome, considered such responses as carbon balance in high-latitude coniferous forests to elevated carbon dioxide levels.

Studies of the leaf economics spectrum in extant plants (Wright et al., 2004) have revealed nonlinear correlations among leaf morphological and physiological characteristics arrayed along a single rate spectrum. At the extremes, what Wright et al. (2004) call quick-return leaves are characterized by high nutrient concentration, high photosynthetic and respiratory rates, short life spans, and low biomass per unit area; at the slow-return end are leaves with low nutrient concentrations, long life spans, low photosynthetic and respiratory rates, and high investment in biomass per unit area (usually in antiherbivore tissues). Correlations of these traits with climate were present, especially when constrained by biome or growth-form/functional group. Wilf et al. (2001) used these morphological traits to estimate leaf life spans and position within the economics spectrum for late Paleocene and Early to Middle Eocene dicotyledonous angiosperm leaves, and found close correlations among herbivory and inferred plant defenses in response to independently assessed changes in paleoclimate. Royer et al. (2005) used and extended these morphological-physiological correlations. Based on a preliminary study (Huff et al., 2003), Royer et al. (2005) quantified univariate correlations among leaf traits and demonstrated statistically significant patterns (number of teeth, perimeter ratio, shape factor, and margin percentage); this latter study also demonstrated several relationships between leaf physiognomy and leaf economics. From these results, Royer et al. (2005) developed a set of refined leaf-climate models using multiple linear regressions.

The NLR approach to study of extinct plant physiology has been applied to various plant groups from different times in Earth's history. Perhaps the most explicit comparisons have been made by Feild and colleagues, who have combined studies of angiosperm phylogeny with physiology to examine

likely physiological traits of evolutionarily basal angiosperms (Feild et al., 2000, 2001, 2003a, b). In the deeper past, Phillips and DiMichele (1992) considered the consequences for arborescent isoetalean lycopsids of CAM metabolic pathways, which have been found in modern isoetaleans (Keeley & Busch, 1984) and also inferred from carbon isotopic analysis (Raven & Spicer, 1996). Boyce and colleagues (Boyce & Knoll, 2002; Zwieniecki et al., 2004; Boyce, 2005) examined the physiological attributes of leaves and their xylary support systems in modern seed plants and pteridophytes as indicators of possible constraints on the evolution of leaves in primitive gymnosperms and ferns. As part of this, Boyce et al. (2004) examined the physiology of tracheid lignification in a phylogenetically diverse sample of extant vascular plants. They postulated trade-offs between hydraulic transport and support as the evolutionary driving force of lignification patterns. Lignified tracheidal cells are found in plants with small leaves or leaves with needle-like construction. In those plants with larger laminate leaves (ferns and angiosperms), lignification of tracheidal cell walls is decreased, enhancing water transport, with support functions shifted to heavily lignified fiber cells for support.

GROUND-TRUTHING CLIMATE MODELS

Inferences about climate based on plant physiognomy and ecological tolerances casts plants as natural, independent sources of information with which to ground-truth global climate models at continental, hemispherical, and global scales. Such an approach was used by Wing (1991) in a critique of computer models (Sloan & Barron, 1990). The presence of large nonburrowing tortoises, palms, tree ferns, and dicot trees lacking strong seasonal growth rings in Late Cretaceous and Paleogene deposits of western interior North America was considered incompatible physiologically with sustained below-freezing winter temperatures and a high degree of seasonal temperature fluctuations predicted by the models. Wing (1991) extended the biological argument to the entire Tertiary prior to ca. 34 Ma. He found paleontological evidence to be compatible with the climate-simulation parameters in only one instance for the Paleocene and later Eocene. More recently, Fricke and Wing (2004) have evaluated both LMA and stable isotopes, from phosphate in mammalian tooth enamel and freshwater fish scales, to estimate the MAT in the Early Eocene across a North American latitudinal gradient from Ellesmere Island to Texas. They acknowledge that even in areas where both megafloral and megafaunal assemblages occur in

the same stratigraphic section, these are rarely preserved within the same bed (same chronostratigraphic horizon; this also applies to the entire Phanerozoic record). Furthermore, it is difficult to make direct statistical comparisons in MAT between different paleogeographic areas due to age uncertainties because MAT can change significantly over short periods of time (Milankovic time scales). Contrary to the straight-line application of Recent correlatives between these parameters, Fricke and Wing (2005) demonstrate that the oxygen isotope–MAT correlation during the early Eocene was significantly different from the climate proxies obtained through LMA ($\delta^{18}\text{O}$ estimates were 0.2°C to 2.1°C higher). They also found that the absolute values for $\delta^{18}\text{O}$ differed between the Bighorn, Green River, and Powder River basins of Wyoming, implying that different hydrological regimes existed in these areas. Regardless, this combined approach toward paleotemperature estimates captured a global-warming event at the Paleocene–Eocene boundary not determinable from paleobotanical data alone.

Deeper time climate models are more problematic simply because both abiotic and biotic sources of data are more remote, meaning sparser data, limited modern proxies with which to compare, poorer regional stratigraphic-temporal correlations, and, in some cases, exacerbation of a basic lack of understanding of the complexities of the Earth-climate system. Nonetheless, it is possible to combine geological data and paleontological data in the search for common patterns, allowing climatic inferences based on physical data to be compared to biological changes (e.g., Montañez et al., 2007; Poulsen et al., 2007). Late Paleozoic changes from a cool to warm Earth (Gastaldo et al., 1996) serve as an example of this kind of study. During the Permian, Southern Hemisphere deglaciation occurred in a stepwise pattern, inferred from stable isotopes of marine (Veizer et al., 1999) and paleosol (Royer et al., 2004) carbonates of Euramerica. Three glacial and interglacial pulses have been identified, each distinguished by a $\delta^{18}\text{O}$ excursion, with glacial ice present during the late Gzhelian–Asselian (Carboniferous–Permian), across the Sakmarian–Artinskian boundary, and during the Kungurian–Roadian. Complete Gondwanan deglaciation occurred during the Middle Permian (Roadian), although there are some suggestions of later minor ice pulses (Fielding et al., 2005). Preliminary estimates of atmospheric carbon dioxide concentrations suggest that Permian pCO_2 was up to 10 times greater than during the Late Carboniferous, in which a pCO_2 concentration of ~ 350 ppm parallels the present atmosphere (Montañez et al., 2007). A complex spatio-temporal vegetational re-

sponse to these cycles and overall increasing pCO_2 is recorded in tropical paleolatitudes of the southwestern U.S.A. This pattern shows a trend from wetland megaflores to those that grew under more seasonal rainfall patterns, many elements of which are typically thought characteristic of the Late Permian and Mesozoic (DiMichele et al., 2001a). The overall megafloral compositional changes are similar in western North America and Central Europe, although correlation problems prevent exact comparisons of timing (Scott, 1980; Kerp & Fichter, 1985; Broutin et al., 1990; DiMichele & Aronson, 1992). Overall, this combined geological-paleontological approach demonstrates a close correlation of changes in the abundances of major groups of plants and inferred changes in atmospheric CO_2 , soil moisture, and regional temperature. Major changes in landscape patterns occur at each inflection point of the pCO_2 record rather than at stage boundaries (Montañez et al., 2007), as suggested by global diversity compilations (e.g., Rees et al., 2002). Continental-scale patterns provide insight into the combined effects of changing global climate and paleogeography. However, finer sequence-scale analysis within the regional sedimentological, chronostratigraphic, and geochemical framework captures the nuances of terrestrial ecological response to perturbation.

BIODIVERSITY PATTERNS IN SPACE AND TIME

Applications of synecological analyses have primarily been focused on diversity studies at the continental, hemispherical, and global scales. In general, the systematic diversity of collection sites across an area of interest has been compiled into databases (e.g., The Paleobiology Database, 2007), with all floras binned within a stratigraphic interval (usually stage-level). Spatial and temporal changes can then be evaluated to identify patterns of diversification, range extensions (or contractions), and ecological assembly.

The best resolution of paleobiogeographic patterns is in the extensive Tertiary plant-fossil record, in which there are many extant angiosperm families. The quality of this record has led to many recent studies of group origination patterns, diversification, and range changes relative to present biogeographic distributions (e.g., Tiffney & Manchester, 2001). It is beyond the scope of this review to document all that has been published relative to angiosperm paleobotany in these respects. A few illustrative examples will suffice to demonstrate major research approaches.

Recently, Corbett and Manchester (2004) evaluated the stratigraphic and paleogeographic distribution of *Ailanthus* Desf., a Northern Hemisphere genus commonly encountered as fossils in lake sediments

associated with temperate evergreen taxa. The oldest megafloral remains are known from the Early Eocene of North America and Asia, with the genus appearing in Europe by the Middle Eocene and ultimately achieving a circumboreal distribution. Presently, *Ailanthus* is restricted to the Indian subcontinent, Southeast Asia, the Indonesian archipelago, and northern Australia (violating Wallace's line). Corbett and Manchester (2004) conclude that *Ailanthus* either originated in the Northern Hemisphere and subsequently extended its range southward, or vice versa. Macrofloral evidence exists for the former but is suspect for the latter (there is a dearth of fossil evidence in these geographies). Any attempt to resolve this dilemma would require the use of a molecular phylogenetic analytical approach that may provide evidence for the ecological limits of the ancestral lineage.

Such an approach has been taken by Xiang et al. (2005, 2006) for *Cornus* L. They combined DNA data with morphological traits of extant and extinct taxa. From an extensive set of analyses (PAUP [maximum likelihood], parsimony, and Bayesian phylogeny inference and divergence-time analyses), they conclude that *Cornus* underwent five sequential intercontinental dispersals since origination in Europe. During the late Paleocene, its range expanded into North America via the North American land bridge, with separation and climate forcing isolation (*C. sessilis* Torr. ex Durrand, western U.S.A.) and extinction (eastern and central North America). Range extension occurred into Africa at about the same time, with these taxa retaining an evergreen habit in tropical montane-evergreen forests of eastern Africa. Europe-to-Asia transferral occurred twice, in the mid-Oligocene and mid-Miocene, arriving on this continent also as an evergreen lineage. Documentation of such phylogeographical histories and assemblages becomes the basis for understanding ecosystems and their responses to perturbation (e.g., Collinson & Hooker, 2003).

Extrapolation into deeper time where there are stratigraphic, paleogeographic, and paleoclimatic complications results in much coarser temporal and biogeographic resolution. Rees et al. (2004), for example, used climatically sensitive sediments, plant diversity, and dinosaurs to infer broad geographic patterns for the Late Jurassic (Kimmeridgian and Tithonian, 155.7–145.5 Ma). Using the data compiled by Rees et al. (2000) and plotted within latitudinal bins of 10°, they note low plant diversities in low latitudes where dinosaur remains are well preserved (ascribed to a taphonomic bias and a small number of localities), increasing diversity toward the midlatitudes, and a pole-ward diversity decrease (where megafaunal elements are virtually unknown). High-midlatitude diversity forests were

dominated by a mixture of conifers, cycadophytes, pteridosperms, ferns, and sphenophytes. This stands in marked contrast with low-latitude xeromorphic vegetation, characterized by microphyllous conifers and cycadophytes, and polar assemblages dominated by macrophyllous conifers and deciduous ginkgo-phytes. Although it was only possible to delimit coarse spatial (continental and latitudinal) and temporal (Kimmeridgian, 4.9 Ma; Tithonian, 5.3 Ma) resolution of these vegetational assemblages, they conclude that “an immense biomass and diversity of dinosaurs was apparently supported by sparse vegetation” (Rees et al., 2004: 649) occupying a tropical savannah biome (Rees et al., 2000).

A similar stage-based approach was taken by Rees et al. (2002) for the transition from icehouse to greenhouse conditions in the Permian (Gastaldo et al., 1996), taking into account the northward movement of continents over this interval. Plant-assemblage diversities were compiled at the generic level using taxonomic lists taken from the literature for the Sakmarian (285–280 Ma) and Wordian (267–264 Ma; Rees et al., 1999). These were used in conjunction with dry and wet climatically sensitive lithologies to interpret polar-to-equatorial climate gradients within each stage. To limit spatial and temporal averaging, megafloral data were restricted to inter-locality distances of ca. 100 km and vertically restricted throughout the stratigraphies. The resultant Sakmarian data set consisted of 112 genera from 128 localities (799 occurrences); the Wordian was comprised of 104 genera from 147 localities (1001 occurrences). From these data, nine biomes (tropical ever-wet to tundra) were identified, and the morphological adaptations of the plants within each biome were used to infer precipitation and temperature patterns within the established paleogeographical context. Biomes were compared against computer climate-generated biome models run at two levels of pCO₂ (4×, 8×) to assess the credibility of the interpreted distributions. Rees et al. (2002) found that biome simulations run at elevated pCO₂ matched the empirical data in the equatorial, midlatitudes, and northern high latitudes, although no simulation reproduced the temperate climates in high southern latitudes where alpha diversity is limited to fewer than 15 taxa (Rees, 2002). As Rees (2002) notes, each regional pattern is a reflection of sampling and the effects of regional-level geographic and climatic changes (wet to more seasonal) on different taxa growing in different biomes. In addition, perturbations, extinctions, and turnover at the sub-stage level play a significant role in the perception of broad regional patterns when these assemblages are amalgamated.

PHYLOGENETIC ANALYSES IN PALEOECOLOGY

Accounting for the effects of history on ecological patterns and dynamics is rapidly growing in importance. Attempts have been made both to accommodate and to remove the effects of historical patterns in ecology, by considering both phylogenetic relatedness and biogeographic history. The integration of phylogenetic pattern in the analysis of ecological pattern and process leads inexorably toward further consideration of the fossil record. Fossils not only provide direct evidence of the combinations and distributions of extinct organisms, but also permit dating of nodes in cladograms (Crepet et al., 2004), which may prove important in determining when, where, and under what environmental conditions clade ecological traits may have been established. Conversely, if clade membership strongly affects local ecological structure, it may be difficult to examine patterns of convergence among ecosystems from different times and places, and thus, clade membership attempts to account for phylogeny by recasting ecological descriptions in terms of functional groups or ecomorphs.

INCLUDING PHYLOGENY

In neoecology, the consideration of phylogeny has led to findings that contradict traditional views of plant ecological variation. One need not look far to find the opinion that all plants do the same thing, and, hence, much convergence in ecological patterns is to be expected across widely unrelated lineages, rendering history unimportant. However, work such as that of Ackerly (1999), Webb (2000), or Prinzing et al. (2001), for example, or in a number of papers (e.g., Cavender-Bares et al., 2006; Kembel & Hubbell, 2006; Silvertown et al., 2006) in a special issue of the journal *Ecology* devoted specifically to this subject (Webb et al., 2006), suggests that ecological distributions of species or higher taxa tend to be more clustered with regard to spatial and habitat conditions than expected by chance. Thus, all plants are not doing the same thing and there may be strong phylogenetic and other historical effects on biodiversity and the ecological mediation of evolutionary patterns. Such integration of explicit historical considerations and ecological patterns and processes appears to be an area with tremendous potential to have wide, profound effects on many aspects of ecology (see summaries and comments by Webb et al. [2002, 2006], Ricklefs [2006], and Westoby [2006]).

There are some paleoecological studies that have examined or considered ecological patterns in light of phylogenetic patterns. Examples at a relatively finely resolved taxonomic scale include Burnham's study of

early Cenozoic elms (1983, 1986), in which the major genera of the subfamily Ulmoideae were characterized morphometrically and with respect to their climatic, particularly temperature, tolerance ranges. In each of three genera, species-level diversifications were found to occur during times of climatic instability in the late Eocene. However, new species had the same basic climatic tolerances as both the ancestral forms and those found in the living representatives today, suggesting strong phylogenetic niche conservatism at the clade level. In a study of another Cenozoic member of the Ulmaceae in the subfamily Celtoideae, *Cedrelospermum* Saporta, Manchester (1989) found that the several known species of this genus were typically colonizers of areas disturbed by volcanic ash deposition; some extant members of the Celtoideae share this peculiar ecology. Although the edaphic distribution of *Cedrelospermum* was narrow, Manchester notes that it was widely distributed through a variety of climatic conditions. Wing and Hickey (1984) examined the systematics and paleoecology of phylogenetic relationships within the Juglandaceae, focusing on the genus *Platycarya* Siebold & Zucc. They found Tertiary *Platycarya* species to be thicket-forming shrubs characteristic of open, early successional habitats. This particular ecology is characteristic of species of this genus up to the present day.

The use of nearest-living relatives to infer the climatic tolerances of fossils, discussed above (Mosbrugger & Utescher, 1997; Mosbrugger, 1999), makes the implicit assumption that clades are conservative in their ecological tolerance ranges. By looking across a flora instead of using a single species, the coexistence approach to estimate such climatic tolerances of extinct forms (Mosbrugger & Utescher, 1997) adds considerable support to the general assumption of clade conservatism in niche breadth.

From a still broader, floristic perspective, Wing (1988a) examined the origin of Eocene and Oligocene floras in the Rocky Mountains and concluded that derived microthermal lineages, those typical of cooler, more climatically seasonal climates, originated in high-elevation areas, whereas the lower elevations were dominated by ancestral megathermal (warm equable climate) forms. Once climatic cooling spread throughout western North America, these lineages migrated into and dominated cooler climates that had become widespread through the lowland regions.

Similarly, DiMichele et al. (2001a) found Early Permian floras dominated by phylogenetically derived conifers and cycads, plants previously known only from Late Permian or Mesozoic deposits, associated with a tongue of sediment in the western Pangean equatorial belt deposited during cooler, strongly

seasonal climates, possibly coincident with a last-gasp pulse of high-latitude glaciation (Montañez et al., 2007). Ancestral forms typically grew in more equable seasonal settings.

Both these examples lend support to models that link evolutionary innovation to the crossing of ecological thresholds (e.g., Wiens & Donoghue, 2004; Ricklefs, 2006) and the establishment of basic clade-level ecological traits during these initial radiations.

At a more global spatial scale, the role of history in constraining hypotheses of evolutionary inferences was considered by Manchester and Tiffney (2001) who, again using elms, demonstrated that inclusion of extinct taxa and information on past geographic distributions not only provided more complete phylogenies and added constraining age data, but permitted significant refinement of interpretations on place and conditions of clade origin and evaluation of age and area hypotheses. They conclude that the fullest picture comes from a combination of neobotanical and paleobotanical data within a phylogenetic context.

At the deepest time level, DiMichele and Bateman (1996), Bateman et al. (1998), and DiMichele et al. (2001b) examined the origin of vascular-plant body plans, roughly equivalent to Linnean classes, during the Middle to Late Devonian and concluded that there was strong overlap between phylogenetic affinity and ecological distribution, with lycopsids occupying primarily wetland habitats, seed plants in terra firma habitats, sphenopsids in a narrow range of aggradational settings, and ferns as opportunistic weeds in terra firma environments. Hotton et al. (2002) found evidence of this same basic clade-by-environment subdivision as far back as the Early Devonian, wherein the ancestral clades (zosterophylls and trimerophytes) of the main Late Devonian (and beyond) body-plan groups were already established along the wet-dry-substrate spectrum.

Perhaps the largest scale and most general study to attempt to understand patterns of ecological convergence and divergence is that of Niklas (2006), who compared allometric patterns of biomass partitioning in aquatic macrophytes, bryophytes, and vascular plants, explicitly examining the patterns within a phylogenetic framework. He found a similar pattern of resource allocation to functionally equivalent body parts that are otherwise developmentally distinct and non-homologous in these different groups. From this, he concluded that there may be a single scaling relationship describing biomass partitioning into stem, leaf, and root for all eukaryotic photoautotrophs. This finding, as Niklas (2006) noted, permits the use of simpler, more general model systems to develop analytical solutions to explain biomass partitioning patterns in higher plants. At this level, the inclusion

of explicit phylogenetic consideration leads to the conclusion that at some level of analysis, such considerations can be ignored (see next section).

Similar to studies of allometry within a phylogenetic framework are recent studies of physiology linking fossil and modern plants by Boyce and colleagues (Boyce et al., 2003, 2004; Boyce, 2005), discussed above. This work has permitted convergent patterns in morphology to be identified and linked to underlying physiological controls, revealing certain patterns of trade-off in the basic plant functions, support versus hydraulics. These studies link closely with those of the leaf economics spectrum (Royer et al., 2005, also discussed above), in that plants with small, structurally complex and highly defended, long-lived leaves differ in terms of the lignification patterns in their hydraulic and support systems (having the more primitive condition) from plants with shorter-lived, more physiologically active foliage.

EXCLUDING PHYLOGENY

Just as there have been attempts to include phylogeny and examine the effects of relatedness on ecological patterns, there have been (much more longstanding) attempts to remove such effects. In neoecology, these attempts fall broadly under the study of guilds (Root, 1967; Simberloff & Dayan, 1991) or functional types (Smith et al., 1997). Such approaches implicitly assume that evolutionary relatedness will bias the distribution of plant taxa in space and by resource use pattern, thus impeding comparisons among ecosystems that might otherwise be found to converge (or not) in structure. This approach also aims to make systems comparable in such cases where true morphological convergence exists, but is masked by the use of taxa as the variables by which ecological assemblages are categorized. Functional-type analyses may reclassify plants via multivariate analysis based on their morphological traits, or place them into groups or guilds based on inferred functional roles within ecosystems (Gitay & Noble, 1997; Westoby & Leishman, 1997). This approach may be applied to entire ecosystems as well as to the individual taxonomic components of those systems (Shugart, 1997).

There have been a few paleobotanical attempts to remove taxon effects, an approach that has been used somewhat more extensively in studies of vertebrate paleontology (see Damuth et al., 1992). Wing (1988b; Wing et al., 1992) placed 52 species of Eocene-age flowering plants, gymnosperms, and lower vascular plants into 12 ecological categories based on foliar physiognomy or comparisons with NLRs, basically a guild approach. The subsequent assemblages then were analyzed statistically; structurally distinct assemblages

were found to correlate with different physical habitats. DiMichele and Phillips (1996) rescored Pennsylvanian-age plants according to a suite of ecological traits such as reproductive allocation, body size and form, and dispersal capability. They found that the phylogenetic signal could not be removed; Pennsylvanian wetlands were dominated by several widely distinct phylogenetic lineages, representing Linnean class and ordinal level groups. Thus, distinct body plans represent different fundamental approaches to being a plant and result in strong partitioning of ecological resources by clade. A similar pattern was found in the Middle to Late Devonian radiation of vascular plant classes (body plans) by DiMichele et al. (2001b), in which phylogenetic patterns, ecomorphic (functional type) distributional patterns, and ecological distributional patterns were found to overlap strongly, meaning that historical-phylogenetic patterns could not be removed except to separate ground cover from canopy and understory plants. Thus, functional-type categorizations of angiosperm-dominated systems appear to contain more convergences than those of the Paleozoic, where different kinds of ecosystems were dominated by phylogenetically widely disparate groups. This is an area where more examination is needed and one that should tell us much about evolution and the nature of ecological resource use and occupancy.

INTEGRATIVE STUDIES

EVOLUTION AND ECOLOGY

The conjunction of evolution and ecology has long been sought after. Yet, the two have long been practiced largely separately, despite such pithy characterizations as Hutchinson's (1965) ecological theater and evolutionary play, or Dobzhansky's (1973) classic observation that nothing in biology makes sense except in the light of evolution. Certainly, explicit linkage is more common in neobiology than in paleontology, if for no other reason than the vast differences in the number of practitioners. Nonetheless, because paleontologists are faced relentlessly with evolutionary and ecological history and their contingencies, there have been many attempts to bring them together at all scales from individual structural features to particular species to major groups.

Perhaps the best known example in paleobotany of the quest for an ecological explanation of evolutionary pattern is the origin of the angiosperms, Darwin's abominable mystery. In fact, this group is no more unheralded in its appearance than many of the major classical Linnean plant ordinal or class-level body-plan clades; there are just so many angiosperms around today to attract our attention. And, despite

intensive study of seed-plant phylogeny over the past 20 years, a consistent, agreed-upon sequence of morphological transformations linking the angiosperms to the other seed plants has not been reached (e.g., Hilton & Bateman, 2006, for review). Thus, the angiosperms are representative, almost iconic, in fact, of an evolutionary problem—the origin of major morphological discontinuities. Explanations vary all over the conceptual map, and, still again, the subject is too complex for a comprehensive review here (see Feild & Arens, 2005). The implicitly gradualist hypothesis of a long-shrouded upland origin (Axelrod, 1952, 1972; Stebbins, 1965) visualized aridity as the driving selective force. A more sophisticated version of this model, making fewer assumptions about the tempo and mode of evolution and taking a more critical look at early angiosperm life histories, identified early angiosperms as weedy opportunists confined to river corridors, where they may have moved into areas of reduced competition in lowland settings from a place of origin in drier, marginal, extrabasinal habitats, also characterized by low competition (Hickey & Doyle, 1977). Taking a similar view, that physiological stress was the driving force of angiosperm morphology, but with an opposite viewpoint on where the selection occurred, Retallack and Dilcher (1981) put forth a coastal hypothesis, arguing that early angiosperms moved up from the coast rather than down from the uplands. In a modification of the upland weed model, early angiosperm evolution was hypothesized to have occurred directly within disturbed lowland habitats (Taylor & Hickey, 1992). Most recently, Feild and colleagues (Feild & Arens, 2004; Feild et al., 2004) have attempted to integrate physiological analyses of phylogenetically identified basal angiosperms (e.g., Feild et al., 2003a, b) with the fossil record. They suggest that disturbance and browsing by large vertebrates, specifically dinosaurs, in forest-shaded understories suppressed slower-growing ferns and gymnosperms and permitted rapidly growing, more physiologically escalated, angiosperms (*sensu* Vermeij, 1987) to make significant gains in resource occupancy. Labeling their hypothesis dark and disturbed, they note that the concept of key innovation in this instance is unlikely and that angiosperm dominance is a product of the overlap of a series of essentially unrelated factors.

Considerable evidence has accumulated from Late Paleozoic deposits, suggesting that novel body plans originate in areas of reduced competition, marginal to basinal settings, in effect lending credence to earlier models of upland (in reality, extrabasinal) origin of novelties, but without the presumption of long periods of gradual, microevolutionary change (recall the geological context, in this case the continental strati-

graphic record discussion, above). Most of this evidence comes from the appearance of scrappy, allochthonous remains of plants from derived clades (such as conifers, peltasperms, cycads, and corystosperms) in association with basinal wetland floras dominated by primitive lineages (such as lepidodendrid lycopsids, medullosan pteridosperms, marattialean tree ferns, and calamitean sphenopsids). For example, conifers first appear in the Middle Pennsylvanian, but only as bits and pieces of transported material, usually in basins proximate to tectonically active upland areas (Scott & Chaloner, 1983; Lyons & Darrah, 1989). Later floras rich in these xeromorphic plants occur in rare beds, intercalated within sequences otherwise characterized by dominance of wetland plants, with little overlap in taxonomic composition between these two kinds of floras. Ultimately, these initially extrabasinal, seasonally dry floras become the predominant vegetation in the basinal lowlands, correlating with directional changes in climate (Broutin et al., 1990; DiMichele & Aronson, 1992). The pattern repeats again as yet additional floras and vegetation types appear consisting of even more derived elements (DiMichele et al., 2001a, 2004; Kerp et al., 2006); in these examples, the derived plants often had been known only from much younger rocks, even of Mesozoic age, prior to their discovery in rare Paleozoic assemblages.

At the more detailed level of specific organisms, studies of fossil-plant biomechanics, when combined with stratigraphy and phylogenetic analyses, permit the evaluation of morphological trends in light of ecology. Examples, discussed earlier, include such things as the response of plant-growth architecture to wind shear via the evolution of stem structural safety factors (Niklas & Speck, 2001), or the filling of morphospace, considered in light of plant functional morphology (Niklas, 1999, 2000).

VEGETATIONAL RECOVERY FROM MEGADISTURBANCES

Studies of modern vegetational distribution along altitudinal and latitudinal gradients (Walter, 1985), and responses of past vegetation to climatic change during the Holocene and Pleistocene, demonstrate that plant distribution tracks climate and that plants respond to climatic changes rapidly (see reviews by Post, 2003; Parmesan, 2006). The boundaries of modern and past biomes may simply reflect the position and boundaries of major atmospheric circulation cells (Ziegler et al., 2003). In addition, there is evidence from the deep past that megadisturbances, such as the massive Cretaceous–Tertiary boundary bolide impact, had their greatest effects by changing climatic conditions, even if just for the short term and

in locally variable ways. Furthermore, there are theoretical reasons to suspect that rapid changes in vegetational composition and structure could represent regime shifts, rapid changes from one stable compositional state to another once an environmental/climatic threshold is crossed (Scheffer & Carpenter, 2003; Ives & Carpenter, 2007).

The pre-Pleistocene record contains many well-studied examples of major changes in biotic composition in response to catastrophic (effectively instantaneous), rapid-directional, or prolonged-directional environmental change. The following are examples of some of the major events.

The onset of the Carboniferous ice age in the Mississippian is coincident with the development of widespread wetland floras and the demise of vegetation dominated by the most primitive seed plants (Pfefferkorn et al., 2000; Cleal & Thomas, 2005).

Major reorganization of tropical wetland vegetation of Euramerica occurred at the middle-late Pennsylvanian (Moscovian–Kasimovian) boundary, after millions of years of stability in the face of glacial-interglacial fluctuations (Pfefferkorn et al., 2000; DiMichele et al., 2002; Falcon-Lang, 2004), probably in response to rapid global warming (Phillips et al., 1974; Pfefferkorn & Thomson, 1982; Phillips & Peppers, 1984; DiMichele & Phillips, 1996; Cleal & Thomas, 2005). This may have been caused or exacerbated by tectonically driven elevational changes in Central Europe, which would have liberated large amounts of buried carbon and reduced the areas of carbon burial in the tropics (Cleal & Thomas, 2005). Middle Pennsylvanian-type wetland vegetation persisted through the Permian in China (Wang & Chen, 2001), where it remained very wet due to proximity to moisture sources and atmospheric circulation patterns (Ziegler, 1990). Dominance of weedy vegetation and a period of chaotic dynamics follow the Euramerican regional extirpations (Peppers, 1979, 1996; Pfefferkorn et al., 2008).

Vegetational changes in the dominant biome in most of equatorial Pangea occurred across the Carboniferous–Permian boundary (Kerp & Fichter, 1985; Broutin et al., 1990; DiMichele & Aronson, 1992) in response to long-term changes in temperature and rainfall patterns, again perhaps linked to changes in the extent of glacial ice and atmospheric CO₂ (Montañez et al., 2007).

Terrestrial and marine biotic changes near the Permian–Triassic boundary, in response to complex causation (Erwin, 1993), resulted in long pseudo-successional recovery lags and wholesale vegetational restructuring (Looy et al., 1999), with evidence of persistence of many forms in extrabasinal areas (Kerp et al., 2006).

Major vegetational restructuring and species turnover occurred at high latitudes (and possibly globally) at the Triassic–Jurassic boundary (McElwain et al., 1999) apparently caused by a rapid 3%–4% increase in atmospheric CO₂.

The Cretaceous–Tertiary boundary had profound effects on terrestrial vegetation globally. Initially debated with regard to extent and rapidity of plant response (Hickey, 1981; Tschudy, 1984), it is now clearly documented to be rapid (Johnson, 1992) and global, but with variation dependent on local and regional climate and topography (Wilf & Johnson, 2004). Followed by what may have been a pseudo-succession similar to that of the early Triassic (Wolfe & Upchurch, 1986, 1987), like that former event, it appears that lowlands may have been more homogeneous than was characteristic of extrabasinal areas, indicated by rare finds of distinct and diverse floras (Johnson & Ellis, 2002). Significantly different interactions between plants and animals may have ensued, delaying the radiation of large mammals for millions of years (Wing & Tiffney, 1987).

A short, extreme pulse of global warming at the Paleocene–Eocene boundary, the so-called Paleocene–Eocene thermal maximum (PETM), was driven by rapid global warming, which correlates with sharp changes in carbon isotopic composition of marine sediments (Zachos et al., 2005). Vegetational response was rapid and accompanied by large range shifts (Wilf, 2000; Wing et al., 2005). Finally, long-term climatic cooling occurred from the late Eocene through the early Oligocene (see papers in Terry & Evanoff, 2006) and was accompanied by vegetational changes that effectively tracked the changes in climate (e.g., Jaramillo et al., 2006).

Although each of these changes is unique, comprising different taxonomic compositions and different causes, either in kind or in degree, and occurring under different continental configurations and prevailing climates, there are unmistakable similarities. First, all confirm that vegetation responds rapidly to environmental changes, be those changes in extremes or seasonal distribution of temperature or rainfall. Long-term climatic changes demonstrate that plants, particularly if considered at the scale of biomes or large-scale species pools, track climate relatively closely and faithfully. Often, this is accompanied by intrabiomic changes in dominance-diversity while retaining much of the basic species-pool presence-absence composition. Rapid to catastrophic changes are almost always accompanied by dominance of opportunistic weedy vegetation during the initial response. In some instances, this vegetation gives rise to persistent dominant forms, though, in most cases, it is rapidly replaced by more K-selected

growth forms. Pseudo-successions follow several of these events; however, there are indications from occurrences of rare intercalated or precocious floras that more complex and diverse vegetation continued to persist or exist refugially in extrabasinal areas. Thus, such pseudo-successions would be most indicative of long-lasting environmental disruption of the lowland wetlands and inhibition of reestablishment of most surviving lineages from surrounding areas. Finally, these events indicate that plants and vegetation can and do survive major environmental changes, but that recovery from these disruptions generally takes millions of years (e.g., plants typical of Mississippian seasonally dry habitats reappear in similar habitats during the late Pennsylvanian and Permian [Mamay & Bateman, 1991; Mamay, 1992]; plants of Mesozoic habitats appear precociously in the Paleozoic [DiMichele et al., 2001a; Kerp et al., 2006]; dominant conifers both occur precociously in the Pennsylvanian and survive the Permo–Triassic extinction though returning after a long lag [Lyons & Darrah, 1989; Looy et al., 1999]). It must be reiterated that apparent stratigraphic lags in the occurrence of taxa are impacted by the regional and basinal processes operating on preservation potential of organic matter (see sequence stratigraphic discussion above; Gastaldo et al., 2005).

PLANT-ANIMAL INTERACTIONS

Our coverage of this expanding field of paleoecology will be abbreviated because most of the research focuses on animal paleobiology in which the plants are substrates for animal activities. There are important areas where the ecological attributes of the plants and animals are considered jointly, generally involving comparative phylogenetic patterns.

Insect-mediated pollination biology of angiosperms (and potentially other groups of plants, though there is greater speculation there) has been an area where some debate has arisen due to potential conflicts between theory and data. Crepet (1979, 1985) suggested that the coevolution of angiosperms and faithful insect pollination during the Cretaceous was a powerful driving force both in the evolution of the flowering plants and of their pollinators. Many modern students of insect systematics and ecology have suggested that the expansion of the flowering plants in fact created a substrate for the tremendous radiation of the insects. Labandeira and Sepkoski (1993), in an analysis of the fossil history of insect diversity and timing of origination of functional feeding groups, found that insects radiated significantly earlier than the angiosperms, during the Triassic and Jurassic, and argued for the decoupling

of insect diversification from that of flowering plants. Grimaldi (1999) has challenged this interpretation of no relationship, considering conjointly the fossil record of the major groups of insect pollinators and phylogenies of these clades. He argues that there is strong coincidence in the timing of insect and entomophilous angiosperm radiations. This debate continues (e.g., Labandeira, 2002).

Much of the literature on plant-arthropod interactions has focused on the trace-fossil record of arthropod activity. Most evidence from the earliest land plants suggests that arthropods were acting mainly as detritivores, with only limited evidence for attacks on living plants (Kevan et al., 1975; Labandeira, 1998). By the Carboniferous, there is considerably more evidence for arthropod predation on living plants. The majority of data, such as that from coprolites (Scott, 1977b; Labandeira et al., 1997), suggests that detritivory remained the major way in which plant productivity entered the invertebrate food chain (Scott & Taylor, 1983; Scott et al., 1985). There is some indication that insects were involved in medullosan pollination, based on coprolite data (Scott & Taylor, 1983). Labandeira (2006a) reports that the earliest evidence of external foliage feeding occurs in the Late Mississippian, and that insect herbivory is concentrated particularly on medullosan pteridosperms in tropical floras, also noted by Scott et al. (1992), and on glossopterid seed plants in the Southern Hemisphere. Evidence of distinct forms of feeding, such as piercing and sucking, has also been documented in the Pennsylvanian (Labandeira & Phillips, 2002). During the Permian, in tropical regions, it appears that insect feeding was also concentrated preferentially on certain clades (Beck & Labandeira, 1998; Labandeira & Allen, 2007). Labandeira (2006a) finds two further expansions of insect herbivory, one beginning in the early Mesozoic, and the other taking place in the mid-Early Cretaceous, coincident with the evolutionary radiation of flowering plants. Insects seem to have established modern food-web patterns by the end of the Carboniferous, with the full spectrum of insect functional feeding groups active by the end of the Triassic (Labandeira, 2006b).

The record of vertebrate-plant interaction is more difficult to interpret. Not only might it involve herbivory (Chin & Gill, 1996), which will be considerably more difficult to detect from feeding traces on plants than is the case for arthropods, and detritivory (Chin, 2007), but vertebrates, particularly those of large size, can considerably alter ecosystems through various kinds of disturbance (e.g., transformation of vegetational structure by elephants; Wing & Buss, 1970). The earliest evidence of vertebrate herbivory is from

the later Carboniferous (Hotton et al., 1996; Sues & Reisz, 1998). Interestingly, these early occurrences are not followed by a major radiation of vertebrate herbivores. Based on patterns of taxonomic diversity, there is a diversification lag paralleled by the evolution of herbivorous feeding strategies in insects (Labandeira, 2006a). Some of these early vertebrates had large bodies and small heads, suggesting that they may have been fermentative gut processors. The first vertebrate with indisputable evidence for oral processing of tough, high-fiber plant material is of Late Permian age from Russia (Rybczynski & Reisz, 2001). Prior to the Late Permian, vertebrate communities are dominated by what appear to be carnivorous forms. It is not until the Late Permian that trophic pyramids appear similar to those of modern communities (DiMichele & Hook, 1992; Sues & Reisz, 1998). Many Late Paleozoic seeds are large and have fleshy seed coats; Tiffney (2004) suggests that these fleshy seeds may have been consumed and dispersed by vertebrates, which may have confused them for carrion. However, he also concludes that there is, overall, relatively limited evidence for vertebrate dispersal of most Paleozoic seeds (but recall the disparity of preservational requirements between plant and vertebrate remains).

A deep understanding of the effects of dinosaurs on Mesozoic plant communities has been elusive. It is clear that these large animals would have been major agents of mechanical disturbance and also consumed, probably in an unspecialized manner, a wide spectrum of plants (Coe et al., 1987; Tiffney, 1997; Chin & Kirkland, 1998; Chin, 2007). In addition, they may have been major agents in promoting the expansion of weedy angiosperms (Feild & Arens, 2005). Coevolution with dinosaurs also may have had selective effects that can still be seen today on the chemical and morphological attributes of clades that reached their zenith in the Mesozoic, such as cycads. Many of these plants contain neurotoxins in their leaves, which may have deterred vertebrate herbivory, but not in the (edible) sarcotestas of their seeds, permitting seed herbivory and dispersal (Mustoe, 2007).

Following the demise of the dinosaurs at the end of the Cretaceous, large areas of forest developed in the Paleocene, coincident with a delayed appearance of large-bodied mammalian vertebrates (Collinson & Hooker, 1991); Wing and Tiffney (1987) attributed this suppression of vertebrate body size increase to the vegetational structure. Tiffney (2004), in a review of the role of vertebrates in seed-plant dispersal through time, goes so far as to suggest that only with the demise of the dinosaurs could the angiosperm-bird-mammal dynamic evolve, resulting in a fundamental change in ecological dynamics between the Mesozoic

and Cenozoic. We may presume that Tertiary ecosystems, especially those of the post-Paleocene, functioned much like those of the present with regard to the variety of plant-vertebrate interactions (see the reviews by Collinson & Hooker [1991], Wing [1998], and Tiffney [2004], which bring together much of the literature on vertebrate interaction with plants).

ECOLOGICAL ASSEMBLY RULES IN SPACE AND TIME

The concept of assembly rules in ecology has been debated with varying intensity and in various guises nearly throughout the history of the discipline. The very idea of ecological assembly implies determinism and predictability of outcome—it is the nature of this determinism and the particular nature of the expectations about outcome that lie at, or close to, the root of this long-term controversy. From the time of the long-running Clementsian superorganism (Clements, 1916) versus Gleasonian species individualism (Gleason, 1926) debate over succession and climax communities, to more modern incarnations of this discussion about the degree of interaction and coevolution in communities (e.g., Diamond, 1975; Conner & Simberloff, 1979), to recent more generalized formulations (Weiher & Keddy, 1999), the inference of rules of community assembly, drawn empirically from time-space patterns, persists despite general skepticism (e.g., Foster et al., 1990). General skepticism is drawn from things such as the responses of plants to the retreat of ice following the last glaciation (e.g., Overpeck et al., 1992; Jackson, 2000), or studies of short- and long-term, apparently stochastic, changes in the composition of ecological communities (Hubbell & Foster, 1986). Hubbell's (2001) formulation of a general theory of ecological dynamics, in which species are treated neutrally as identical elementary particles, changes the terms of the debate to a great degree, in that deterministic processes may lead to a variety of outcomes. Furthermore, the explicit consideration of historical constraints on modern ecological patterns, via inclusion of phylogenetics and fossil history (Webb et al., 2006), into the explanatory framework, impinges on the matter of assembly because past events may have impacts far into the future, a basic tenet of assembly-rules considerations.

In deep-time paleontology, there has been little explicit consideration of the matter of ecological assembly rules, primarily because of the need for a sequence of fossil deposits over a specific time interval and covering a spatial extent that would permit evaluation of patterns of species addition sequences and combination patterns to be rigorously evaluated statistically. However, it is the interactions

of populations and individuals that dictate and scale upward into larger ecological patterns (e.g., Hubbell, 2001); surely, such interactions are what also underlie the dynamics of evolution. Thus, it should be expected that evolutionary assembly of vegetation over long periods of time should be under the same basic controls as assembly in space over short periods of time. The most general models for controls on community assembly are summarized by Belyea and Lancaster (1999) and Weiher and Keddy (1999). Using somewhat different jargon, these authors present basically the same hierarchical model, consisting of three components. The model also applies to evolutionary assembly over long spans of time as it does to spatial assembly on post-glacial time frames. The following factors control the composition of any site-specific assemblage. (1) Can a species get to the site? In other words, is it a member of the regional species pool, or "metacommunity" (*sensu*, Holyoak et al., 2005)? (2) Once on a site, can the species survive under the local physical conditions? Does it have the physiological and structural capabilities to exist under the soil edaphic conditions, the local aspect, and the light regime of the site? (3) If the first two criteria are met, can the representatives of the species outcompete representatives of other species already on the site, or those that arrive later? To a certain degree, this subsumes and may largely be a consequence of the effects of incumbency, which are related to population size, likelihood of expropriating resources, likelihood of colonizing unutilized or underutilized resources (e.g., Gilinsky & Bambach, 1987), and fecundity.

The most explicit statement of a model for evolutionary assembly of ecological systems is that of Valentine (1980). This heuristic model describes an adaptive zone as a checkerboard, or a pattern of tesserae through time. Each square represents an ecological niche. The initial population to establish within this landscape finds little or no competition for resources and can survive even if only marginally able to live on the site. Given that most speciation will produce descendants similar to the ancestor, ecological space is gradually filled by new species around the resource space of the initial occupant. Coincident with small-scale evolution are rare larger-scale departures in ancestor-descendant similarity, most of which produce nonviable offspring, but some of which will produce forms that can survive if they can reach and survive in resource spaces with low or no competition. Gradual filling of ecological resource space then begins around these new resource nodes. Eventually, as ecological resource space fills, large-scale departures decline in frequency because their chances of survival decline. This is due to the effects of incumbency within the overall adaptive landscape.

Walker and Valentine (1984) later criticized this model because of the supposed lack of niche saturation in ecospace (see Patzkowsky & Holland [2003] for a similar paleontological perspective), a matter widely addressed in the neoecological literature. In addition, the static view of niche space comports neither with the way in which niche generally is conceived (Whittaker et al., 1973), that is as defined by species rather than as preexisting, nor with the similar, expanded view, known as niche construction (Odling-Smee et al., 1996), which argues that organisms, by their actions and interactions, create and expand niche/resource space. Nonetheless, the Valentine (1980) model, though in need of modification, is still a strong basic framework for uniting evolutionary models of ecological assembly with mainly spatial neoecological models. DiMichele et al. (2001b, 2005) have applied some aspects of these models to the examination of ecological assembly patterns in Paleozoic plant communities.

An entirely different way of examining ecological assembly and the rules by which plant assemblages may be structured is emerging from the study of plant allometry. In short, beginning with metabolic scaling theory (West et al., 1997; Brown et al., 2004), a straightforward set of linkages has been developed among plant size, mass, metabolic rate, etc., all the way to spatial-density aspects of populations and mixed-species stands (Enquist et al., 2002, 2003, 2007; Niklas et al., 2003; Niklas, 2006). In the model from West et al. (1997), the metabolic rate of an organism scales to its body mass raised to the 3/4 power. These relationships have been found to apply to the scaling of plant-body size within populations, and from that to entire multispecies plant communities (Niklas & Enquist, 2001; Niklas et al., 2003). In its most fully elaborated form (Enquist et al., 2007), these scaling laws permit basic physiological attributes of organisms to be linked directly to the ecological structure of plant communities in a “taxon-free” manner, given that the basic rules appear to apply to all major groups of eukaryotic photoautotrophs (Niklas, 2006). The strength of this approach, to quote Enquist et al. (2007) “is that it reduces much of the complexity of organisms and ecosystems to simple, but universally applicable, physical and chemical principles.” In certain ways, this approach meshes with Hubbell’s (2001) neutral theory, in that the particulars of species composition do not really matter to ecosystem functioning. Where the fossil record permits (e.g., some of the examples given in Enquist et al. [2007]), the predictions about organism size and stand densities can be tested directly, often in systems for which there is no modern equivalent. Conversely, to the extent that these scaling

generalities are proven to hold (also consider the leaf physiological rate spectrum, discussed above), they may be useful to allow estimation of attributes of ancient systems. The degree to which this approach becomes central to ecology remains to be seen.

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